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INARTICULATE BRACHIOPODS OF THE LOWER AND MIDDLE CAMBRIAN PIOCHE SHALE OF THE PIOCHE DISTRICT, NEVADA[1]

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ABSTRACT

The Pioche Shale spans the Lower-Middle Cambrian boundary as currently recognized in North America. It has yielded a modest inarticulate brachiopod fauna represented by at least nine species from two orders. The following taxa are recognized from the collections of some 2,700 specimens: the acrotretides *Hadrotreta primaaea primaaea* (Walcott), *Hadrotreta primaaea minor* new subsp., *Aphelotreta minuta* new gen. and sp., *Acrothyra minor* Walcott, *Eothele spurri* (Walcott), *Acrothele* sp. 1, *Acrothele* sp. 2, and an indeterminate acrotretid, together with the paterinides *Dictyonina pannula* (White) and *Micromitra* sp.

Changes in the brachiopod fauna across the series boundary between the Lower and Middle Cambrian are small. Among the abundant taxa *Eothele spurri* is confined to the Lower Cambrian *Bonnia-Olenellus* Zone, but both *Hadrotreta primaaea* (Walcott) and *Dictyonina pannula* range from the *Bonnia-Olenellus* Zone into the pre-*Albertella* beds of the Middle Cambrian.

Dictyonina pannula is the most common member of the Paterinida in the lower part of the formation. It is the type species of the genus, is illustrated for the first time photographically, and is redescribed from etched material. Its ventral musculature is now much better known than that of any other paterinide. The distribution of the muscles suggests that the Paterinida are phylogenetically remote from any other inarticulate order.

INTRODUCTION

Late Early Cambrian and early Middle Cambrian brachiopods are not well known, but they are moderately diverse and relatively abundant at several levels in the Pioche Shale of southern Nevada.

Cambrian rocks near Pioche, Nevada, have been studied intermittently since 1871 (White, 1874). The most recent detailed account is that of Merriam (1964), who reviewed the history of earlier geological work in the region and traced the changing terminology of the various formations of the area. Merriam's (1964) stratigraphic

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units are used in the present account, which is based largely on collections made during the period from 1968 to 1970.

The oldest formation in the region was referred to the Prospect Mountain Quartzite by Merriam (1964, p. 9), but Stewart (1974, p. 612) considered the beds to be the Zabriskie Quartzite and the upper and middle members of the underlying Wood Canyon Formation. These rocks have not yielded body fossils, but *Skolithos* occurs in their upper part (Merriam, 1964, p. 11). They are overlain by the Pioche Shale, in which Merriam (1964, p. 17) recognized six members, only two of them being formally named units (Fig. 1).

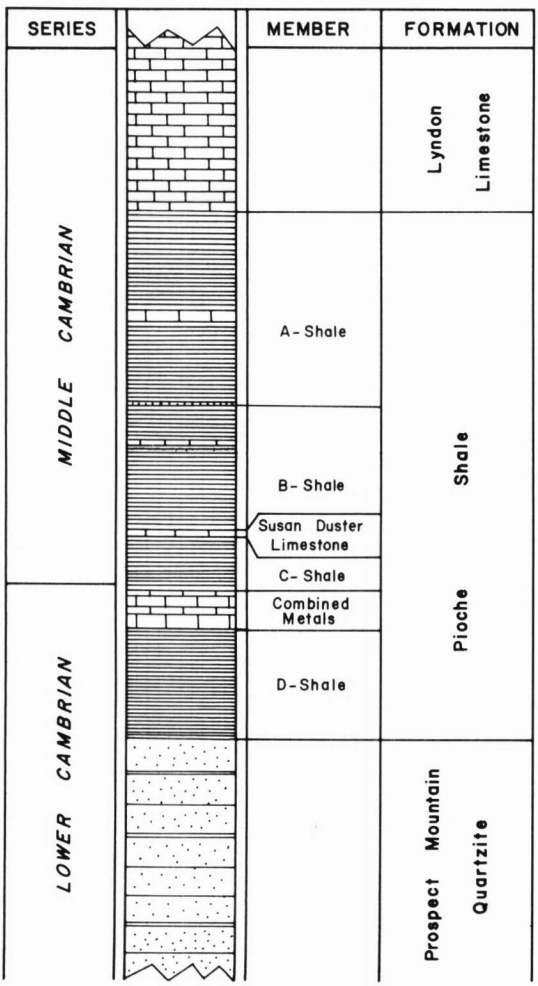

FIG. 1. General stratigraphic relationships of the Pioche Shale and its members in the Pioche district.

Palmer's (*in* Merriam, 1964, p. 26) examination of the fauna of the Pioche Shale showed that the Lower-Middle Cambrian boundary occurs between the Combined Metals Member and the Susan Duster Member: "The few poorly preserved trilobites from the C-shale member are questionably Middle Cambrian."

All of the fossiliferous Lower Cambrian beds are of late Early Cambrian age. The D-shale fauna contains species of *Bristolia, Fremontia,* and *Olenellus;* trilobites of the Combined Metals Member include two species of *Olenellus* together with species of *Crassifimbria, Zacanthopsis,* and *Antagmus* (Palmer *in* Merriam, 1964). These are all elements of the *Bristolia* faunule, which occurs in the uppermost *Bonnia-Olenellus* Zone in eastern California (Nelson, 1976, p. 31).

The Susan Duster Member and the lower part of the A-shale member contain earliest Middle Cambrian pre-*Albertella* Zone faunules. *Albertella* occurs in the upper beds of the A-shales (Palmer, 1971).

A brachiopod was among the first fossils described from the Pioche district. White (1874) erected *Trematis pannulus* from material collected by the Wheeler Expeditions of 1871 to 1873. The same form was discussed by Pack (1906) and the species is now the type of the genus *Dictyonina* Cooper (1942). Walcott (1886, 1891, 1902, 1908) made extensive collections in the Pioche district and the results of these collections were incorporated in his 1912 epic survey of Cambrian brachiopods. He recognized four species of inarticulate brachiopods at Pioche: *Acrotreta primaaea* Walcott, *Acrothele spurri* Walcott, *Acrothele subsidua hera* Walcott, and *Micromitra* (*Iphidella*)*pannula* (White). As was inevitable for the time, Walcott was hampered by the quality of his material, which had to be prepared by entirely mechanical means. Rowell (1966) revised some of Walcott's inarticulate brachiopod species from material prepared by etching in formic acid some of Walcott's original topotype collections. The revision included *Acrotreta primaaea,* which was made the type species of the genus *Hadrotreta* Rowell. The remaining species from Pioche have not been restudied since 1912, but Palmer (*in* Merriam, 1964) noted the occurrence of several brachiopod genera in the Pioche Shale at Pioche.

Acknowledgments.—I am indebted to my

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STRATIGRAPHIC DISTRIBUTION

The brachiopods of the Pioche Shale are of particular interest because the formation spans the Lower-Middle Cambrian boundary as currently recognized in North America. Unfortunately, the series boundary occurs in rocks that are not very fossiliferous, the C-shale member. Some 25 m of these shales separate the uppermost Lower Cambrian brachiopod fauna of the Combined Metals Member from the lowermost Middle Cambrian brachiopods of the Susan Duster Member. Because of the preparation techniques, well-preserved inarticulate brachiopods can be recovered only from limestone. Although occasional specimens occur in shale, they are commonly crushed and, inevitably, cannot be prepared to yield the fine detail readily shown by etched specimens. In spite of this limitation, the data from Pioche, combined with reconnaisance-level observations from several scattered localities ranging from north-central Nevada to southern California, allow some tentative generalizations concerning changes in the brachiopod fauna in this part of the stratigraphic column. Although the details are still elusive, the generalizations are in rather marked contrast to those that may be made for the dominant elements of the polymeroid trilobite fauna.

At Pioche, the upper Lower Cambrian brachiopod fauna is dominated by three species, *Hadrotreta primaaea, Dictyonina pannula,* and *Eothele spurri* (Fig. 2). The fauna has been found at several levels within the top 15 m of the Combined Metals Member. Typically, all three species are present, but there is considerable fluctuation in their relative abundances. *Dictyonina pannula* is commonly the numerically dominant species, particularly in the less fossiliferous collections.

This fauna is widely distributed geographically in upper Lower Cambrian rocks of the western and central parts of the Great Basin (Fig. 3). It occurs with species of *Bonnia* and *Olenellus* in thin limestone beds within the Preble Formation of north-central Nevada (Rowell, Rees, & Suczek, 1979) and is present in a thin limestone bed some 50 m above the base of the Pioche Shale in Fritz's (1968) Campbell Ranch section in the northern Egan Range. At the latter locality it is associated with *Onchocephalus papulosus* Fritz, *Zacanthopsis levis* (Walcott), *Bonnia copia* Fritz, and *Olenellus gilberti*? Meek (Fritz, 1968, fig. 1). It has also been found at several levels within the lower part of the Carrara Formation of southeastern California.

Eothele spurri is not known in beds higher than the uppermost *Bonnia-Olenellus* Zone, but both *Dictyonina pannula* and *Hadrotreta primaaea* range upward into pre-*Albertella* Zone Middle Cambrian strata. The lower stratigraphic range of this assemblage of three brachiopod species is not known with any precision at Pioche because none of the beds underlying its first occurrence in the Combined Metals Member have yielded brachiopods. Elsewhere, what is seemingly the oldest occurrence of the fauna is found on Eagle Mountain in the southeastern Death Valley region of California. Here, thin limestone beds some 20 m above the Zabriskie Quartzite have yielded *Eothele spurri* and *Hadrotreta* sp. in association with the olenellid *Peachella* sp. This horizon correlates approximately with the lower part of the D-shale member at Pioche. Consequently, our present knowledge of the

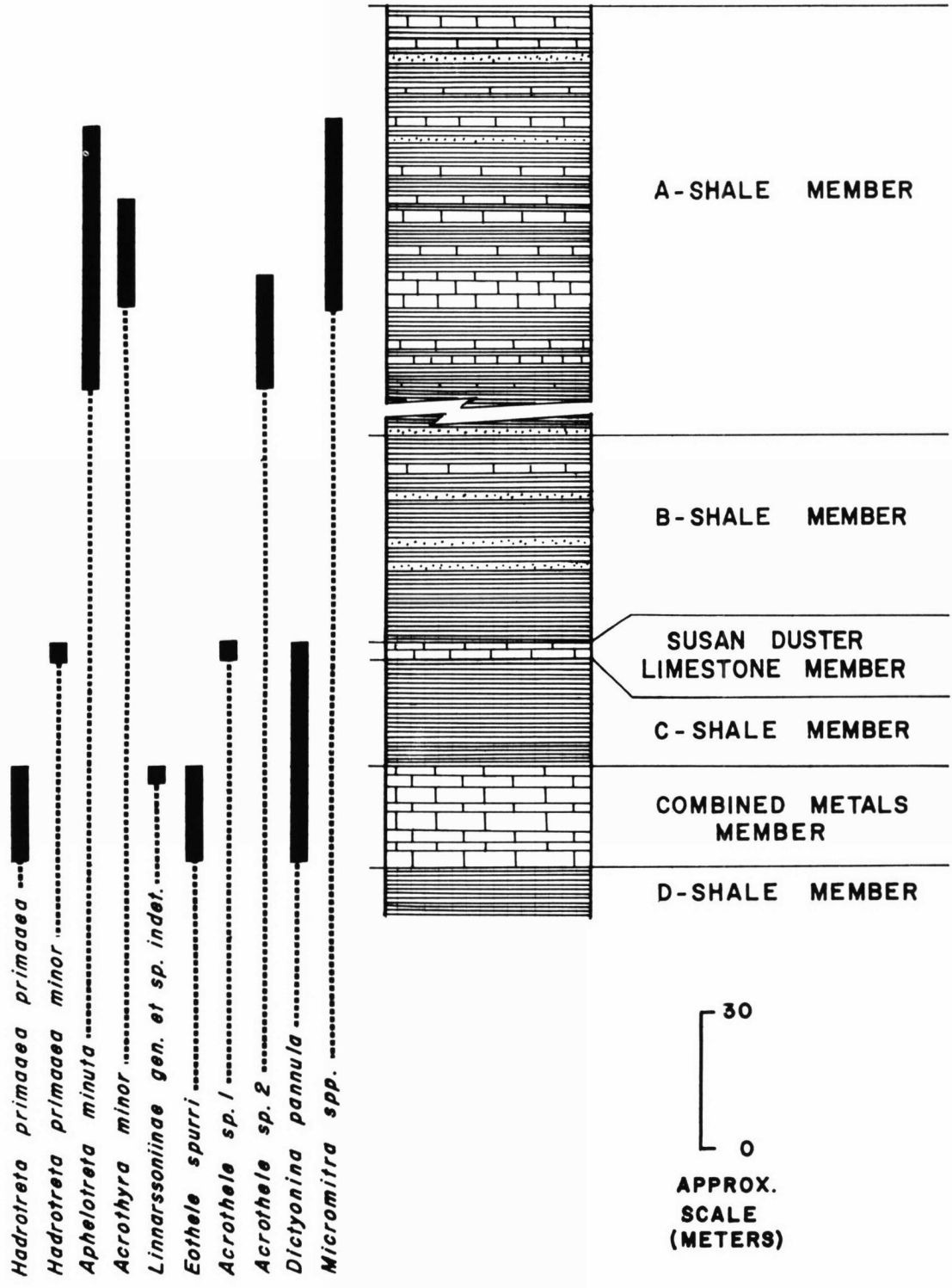

FIG. 2. Composite stratigraphic ranges of the inarticulate brachiopods of the Pioche Shale in the Pioche district. (The lowest 30 m of the A-shale member yielded no brachiopods and are omitted from the section to conserve space.)

stratigraphic range of *Eothele spurri* suggests that it is restricted to the upper part of the *Bonnia-Olenellus* Zone. Its association with *D. pannula* and *H. primaaea* is characteristic of sites of carbonate deposition in the western part of the Great Basin during this time interval.

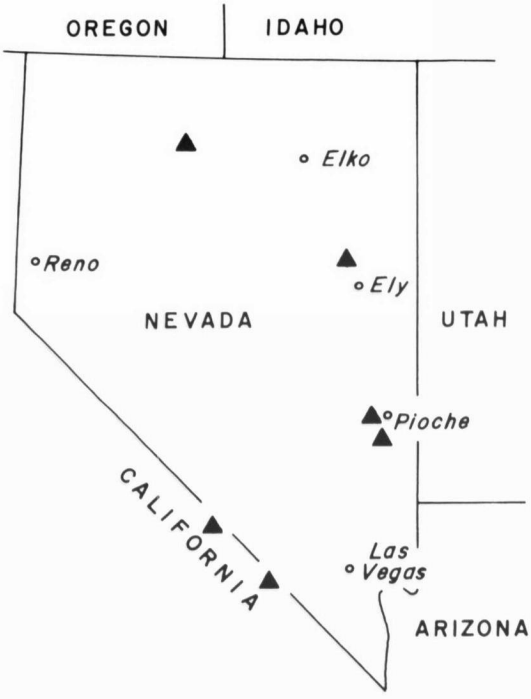

FIG. 3. Geographic distribution of the late Early Cambrian *Hadrotreta, Eothele, Dictyonina* fauna in the Great Basin. Triangles mark locations where fauna has been recorded.

As is well known, there were abrupt changes in the composition of the polymeroid trilobite fauna at the close of Early Cambrian time expressed most dramatically in the extinction of the olenellids. Unfortunately, it is not possible to document this event in any detail in the Great Basin because all of the known sections are either unfossiliferous or only sparsely fossiliferous over the critical stratigraphic interval. Superficially, the extinction of the olenellids is reminiscent of the major extinctions that occurred among polymeroid trilobites at the close of Late Cambrian biomeres (Palmer, 1965; Stitt, 1971), but there are significant differences. The most obvious distinction is that many of the trilobite groups found in association with the olenellids did not become extinct concurrently with the demise of the latter, but persisted into the Middle Cambrian. The cause of the olenellid extinction is unknown. Whatever the cause, it did not have a marked influence on the brachiopod fauna. Although the upper stratigraphic range of *Eothele spurri* approximately coincides with that of the olenellids, the Acrothelidae, the family to which it is referred, flourished in the Middle Cambrian. Furthermore, as previously noted, *H. primaaea* and *D. pannula* range into the lower part of the Middle Cambrian.

In the lowest Middle Cambrian brachiopod fauna at Pioche *D. pannula* is relatively rare, but *H. primaaea* is abundant. Individuals of the latter species are much smaller than the maximum size attained in the Lower Cambrian and are herein treated as a separate subspecies. A further distinction between the uppermost Lower Cambrian and the lowermost Middle Cambrian fauna in the Pioche Shale is the presence of species of *Acrothyra* in the latter. The genus is sparsely represented in the Susan Duster Member and is sporadically present in limestone residues from the A-shale member higher in the sequence. Present information suggests that the genus ranges as high as the base of the Wheeler Shale (*Ptychagnostus gibbus* Zone) of the Great Basin (McGee, 1978).

Two aspects of the Pioche brachiopod fauna are particularly noteworthy. The first is the surprising absence of lingulides. The order was extant because species of *Lingulella* occur in the older Poleta Formation (*Nevadella* Zone) in Esmeralda County, Nevada (Rowell, 1977, p. 78). Nonetheless, not a single valve or identifiable fragment has been found among the few thousand specimens of inarticulate brachiopods recovered from the residues. Clearly the environmental conditions that prevailed during this time interval were not suitable to species of the genus. It is also possible that the environmental preferences of lingulides were much narrower in the Early Cambrian than they were in post-early Middle Cambrian time.

The second interesting feature is that the stratigraphic interval spans the first appearance of the Acrotretidae in North America. *Hadrotreta* from the upper *Bonnia-Olenellus* Zone is presently the oldest known genus. It is difficult to assess the significance of this record. Two obvious alternatives are available: 1) the Acro-

tretidae arose at about this time, or 2) the family had been extant for some previous unknown time but dispersal barriers, or unfavorable environmental conditions, prevented its earlier establishment in the region. Detailed information on the stratigraphic distribution and faunal associations of Early Cambrian acrotretids is not available for most of the world. Indeed, the only comparable data are from Siberia (Pelman, 1977). In that region, *"Homotreta" gorjanskii* (Pelman) and *Linnarssonia rowelli* Pelman are the oldest named species and occur in the middle of the Botomian Stage. These forms are of approximately the same age as the North American *Hadrotreta;* however, an unnamed and undescribed species of *Linnarssonia* is recorded from significantly older rocks of the *Judomia* Zone of the Atdabanian Stage (Pelman, 1977, p. 82). These beds are approximately contemporaneous with the *Nevadella* Zone of western North America (Fritz, 1972) and, if the identifications are justifiable, show that the family Acrotretidae arose earlier than its first known appearance in the western United States.

SYSTEMATICS

Order ACROTRETIDA Kuhn, 1949
Family ACROTRETIDAE Schuchert, 1893
Subfamily ACROTRETINAE Schuchert, 1893
Genus HADROTRETA Rowell, 1966

Hadrotreta Rowell, 1966, p. 12; Aksarina, 1975, p. 91.

When it was erected, the genus *Hadrotreta* was monotypic and its diagnosis and description were based on etched topotype material of *Acrotreta primaaea* Walcott, which was collected at the same time as the primary type specimens. Subsequently, Aksarina (1975) has referred *Hadrotreta pallialis* from the Middle Cambrian of Turkestan to the genus.

Although the original diagnosis of the genus is still accepted (Rowell, 1966, p. 12), new collections made in the approximate region of the type locality alter the known stratigraphic range of the type species. It was initially thought that the type material was of Middle Cambrian age (Rowell, 1966, p. 13). The type locality, USNM locality 31a, was described by Walcott (1912, p. 701) as: "Limestone and interbedded siliceous shales of the Pioche formation, just above the quartzite on the east side of the anticline, near Pioche, Lincoln County, Nevada." Included in the collection from this locality were some early Middle Cambrian trilobites (Palmer, 1965, pers. commun.). Brachiopods etched from other limestone blocks in the collection include both *Eothele spurri* and very large individuals of *Hadrotreta primaaea.* It is now apparent that material from USNM locality 31a was not from one stratigraphic level but spanned at least 25 m of the section. Material from both the Middle Cambrian Susan Duster Member and the Lower Cambrian Combined Metals Member was included in the one sample. The new collections made for this study show that *Eothele spurri* at Pioche is restricted to the Lower Cambrian, and that the type species of *Hadrotreta, H. primaaea,* occurs in both upper Lower Cambrian and lower Middle Cambrian rocks.

The new collections include some of the very early growth stages of *H. primaaea,* and S.E.M. microscopy of the protegulum reveals that the larval morphology of this species differed significantly from that of some Upper Cambrian and Ordovician acrotretid species. The larval protegular shell is pitted (Pl. 6, fig. 1c) in the manner characteristic of Lower Paleozoic species of the family (Biernat & Williams, 1970), but the location of the first-formed pedicle opening is different from that previously observed. In the Upper Cambrian species *Linnarssonella girtyi* Walcott, for example, the larval pedicle opening is restricted to the ventral protegulum. In this species, the foramen is at the end of a low spoutlike projection from the convex protegulum. Biernat (1973) described and illustrated similar relationships in some Ordovician acrotretid species from Poland. In *Hadrotreta primaaea,* however, the pedicle opening was posteriorly located and intersected the margin of the protegulum in all of the specimens examined (Pl. 6, figs. 2c, 4c, 9a). At least during part of its early life the pedicle in this species emerged from between the valves, rather than through an opening confined to the ventral valve. Isolated protegula have never been

described for acrotretids; they are presumably too thin and delicate to survive both the processes of fossilization and acid treatment employed to prepare the material. All the thousands of protegula that have been observed occur as part of the apical region of a postlarval shell. Consequently, it is possible to argue that the marginal position of the foramen on the protegulum in *Hadrotreta* is caused by postlarval migration of the foramen during subsequent growth, the foramen initially having been localized within the protegulum as in *Linnarssonella*. Available evidence does not support such a point of view. The ventral protegulum of *H. primaaea* is typically between 100 μm and 150 μm wide. The smallest valves recovered are about 350 μm wide, yet these forms show no indication of resorption of the foramen (Pl. 6, figs. 4a-c). Furthermore, even the front of the opening is located close to the posterior margin of the protegulum (Pl. 6, fig. 4c). Seemingly, the pedicle of larval *H. primaaea* emerged from between the valves and became confined to the ventral valve subsequently. Shell material was laid down dorsal of the pedicle opening early in the life of the animals because, by the time they were about 500 μm wide, a thin strip of shell, forming the apical tip of the intertrough, separated the foramen from the dorsal valve (Pl. 6, figs. 2c, 9a). In this aspect of its growth, *Hadrotreta* shows similarity with the acrothelids (Williams & Rowell, 1965, fig. 95; Henderson, 1974). The taxonomic significance of this feature is still under study. Preliminary observations of other acrotretids show that this type of ventral valve protegular morphology is not unique to *Hadrotreta* for it also occurs in some species of *Acrothyra* and *Linnarssonia*.

HADROTRETA PRIMAAEA (Walcott), 1902

Figures 4-6; Table 1; Plate 4, figures 8-12; Plate 5, figures 1-10; Plate 6, figures 1-9

Acrotreta primaaea Walcott, 1902, p. 593.
Acrotreta primaeva Walcott, 1912, p. 700, pl. 79, figs. 1, 1a-1f.
Hadrotreta primaaea (Walcott), Rowell, 1966, p. 13, pl. 1, figs. 1-12.

Rowell's (1966) description of the species was based on the limited sample of large individuals available at that time. New collections have provided fresh information, particularly on the younger growth stages, and the ontogeny of the species is now known. Additionally, it is possible to recognize two phena (*sensu* Mayr, 1969, p. 408) distinguished by the markedly different maximum size attained by individuals within a population. For convenience, these two phena are treated as chronological subspecies, but the nature of the boundary between them is unknown. At least locally their stratigraphic distribution has significance; populations with maximum-sized individuals greater than 4 mm wide are confined to the Combined Metals Member; populations none of whose individuals attain widths as great as 3 mm are found only in the Susan Duster Member.

Rowell's (1966) description of adult specimens of the species is followed. Figures 4-6 and Table 1 afford information on the variability with growth of the more readily measured characters and facilitate comparison with other populations.

It is possible that *Acrotreta claytoni* Walcott (1902) is a junior subjective synonym of *H.*

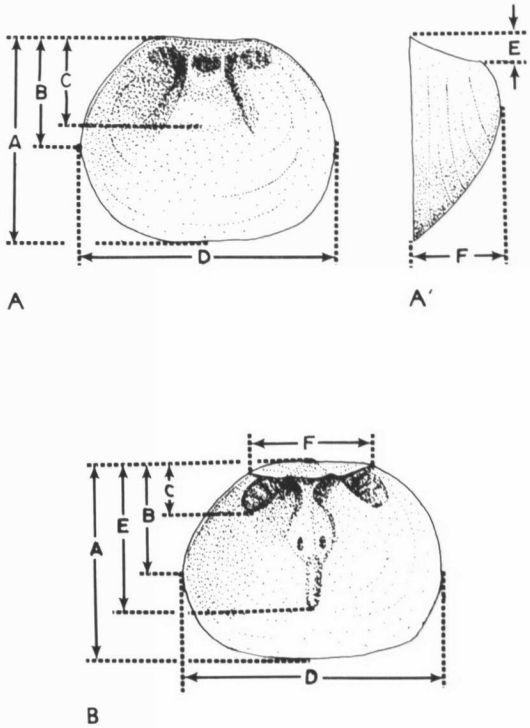

Fig. 4. Diagram of the location of measurements on the ventral valve (A, A′) and the dorsal valve (B) of *Hadrotreta primaaea*.

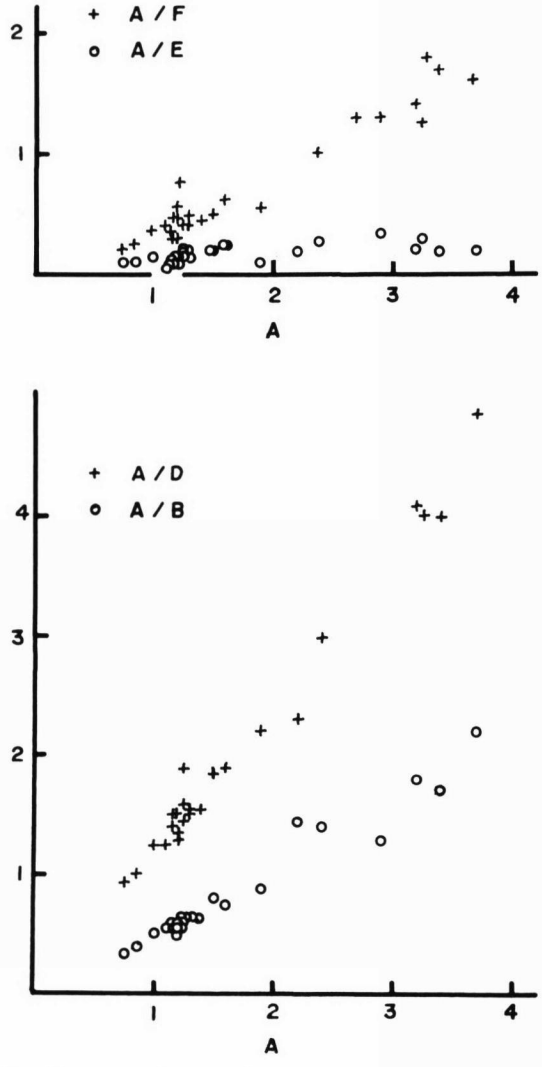

FIG. 5. Scatter diagrams for ventral valves of *Hadrotreta primaaea* from locality R68/186. Measurements in mm; variables as indicated in Fig. 4A.

primaaea. All of the syntypic suite is poorly preserved. The lectotype (Walcott, 1912, explanation of pl. 74, fig. 3) is the only ventral valve in the collection. Its width, height, and length to the line of maximum width agree closely with valves shown in Figures 5A and 5B for specimens of *H. primaaea* of the same length. The only detectable difference between this specimen and *H. primaaea* is in the location of the ventral beak, which is closer to the posterior margin in *H. primaaea*. However, the lectotype of *A. claytoni* is slightly deformed, and even this difference may be an artifact of preservation. Available collections of this species are too small for confident assessment of potential synonymy.

Ontogeny.—The smallest individuals that have been recovered have a length of about 350 μm, about 7 percent of the known maximum size. At this size they would be generically unidentifiable were it not that they form end members of growth series and, in most collections, *H. primaaea* is the only acrotretid represented by adult valves.

Below a length of about 500 μm dorsal valves are gently convex and relatively featureless internally. A minute median plate is typically developed, and supported by a delicate median buttress that extends forward about half of the valve length as an extremely low ridge. At this stage of development the propareas have not appeared and there is no indication of a median ridge. The latter structure is detectable in valves about 700 μm long. It is initally expressed as a low elongate ridge near the midlength of the valve, colinear with the anterior end of the median buttress but slightly separated from it. With subsequent growth, the anterior end of the buttress and the posterior end of the median ridge fuse and the resultant structure forms a single ridge that is higher at its ends than it is at its midlength (Pl. 4, fig. 8; Pl. 6, fig. 5). This condition is typically found in valves between 1 and 2 mm long. As the individuals continued to grow, the dorsal mantle and body wall laid down additional shell material that increased the thickness of the valves. These deposits are particularly heavy just posterior of the center of the valve and the newly added material is broadly convex, rather than ridgelike. Consequently, in this region of the valve, the median ridge appears to be buried under later shell increments (Pl. 5, figs. 6, 9; Pl. 6, fig. 8), and the median buttress and median ridge of large dorsal valves appear as isolated colinear structures separated by a low col forming part of the roof of the valve. The dorsal propareas are commonly first discernible when the valves are about 900 μm long. Although small, their initial shape and disposition are like those of adult valves.

Some of the ontogenetic changes in the ventral valve are more conspicuous than those of the dorsal one, and illustrate problems of identification of subadult acrotretids. The morphological

changes of the immediately postlarval pedicle opening have already been discussed, but by the time the individuals were some 500 μm long they had a foramen confined to the ventral valve in the typical acrotretid manner. Subsequent growth of the ventral pseudointerarea was uneventful. A narrow intertrough extends dorsal of the foramen and separates the two propareas (Pl. 6, figs. 6, 7). The dorsal end of the intertrough seats on the median plate of the opposing valve (Pl. 6, fig. 9).

The most conspicuous changes are internal and are associated with the apical process. When less than 1 mm in length, the internal features are inconspicuous, but a faint, poorly defined thickening of the apical region of the valve, anterior of the foramen, is the incipient apical process (Pl. 4, fig. 9). At this stage of development the posterior surface of the process is parallel with the commissure plane and it rarely shows traces of the apical pits. In valves between 1 and 2 mm long, commonly the posterior surface of the process is gently inclined posteriorly, sloping toward the foramen (Pl. 4, fig. 10; Pl. 6, fig. 3). It is bounded laterally by the trunks of the mantle canals, and anteriorly slopes to the floor of the valve (Pl. 6, fig. 3). With subsequent growth there is an abrupt change in shape of the posterior part of the process. New layers of rather lamellose shell material are laid down and the height of the apical process increases greatly with increasing age. The posterior surface of the process now slopes abruptly to the pedicle foramen, and together with the internal margins of the process, defines a deep cavity (Pl. 5, figs. 4a,b). The internal opening for the foramen is marked by a distinct tube opening into the base of this pit (Pl. 5, fig. 4c). The two apical pits are inserted on the inner surface of the pseudointerarea lateral of the pedicle tube.

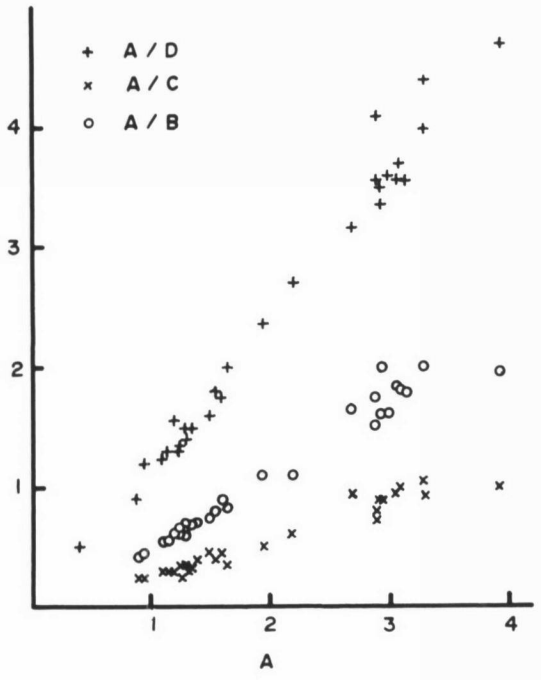

FIG. 6. Scatter diagrams for dorsal valves of *Hadrotreta primaaea* from locality R68/186. Measurements in mm; variables as indicated in Fig. 4B.

HADROTRETA PRIMAAEA PRIMAAEA (Walcott), 1902

Figures 4-6; Table 1; Plate 5, figures 3-10; Plate 6, figures 1-9

Diagnosis.—Largest individuals of population greater than 4 mm in length.

Age.—Late *Bonnia-Olenellus* Zone, Early Cambrian.

Discussion.—Among the collections of nearly two thousand specimens, two distinct phena are recognizable. They may be clearly distinguished only by the maximum size attained by adults. In one of them, *H. primaaea primaaea,* large specimens with width in excess of 4 mm are common. The biggest specimen found was 5 mm wide. The type material of the species belongs to this group. In the other phenon, *H. primaaea minor,* the largest specimens are rarely more than 2 mm wide and never exceed 3 mm. There is no evidence to suggest that the populations lacking large individuals are derived, their large adults having been left elsewhere as a lag deposit. In several collections complete juvenile shells occur and the valves give no indication of transport. Furthermore, the stratigraphic distribution of the phena is significant. All the collections of *Hadrotreta primaaea* from the Lower Cambrian include large adults; none of the samples from the lower Middle Cambrian Susan Duster Member contain individuals wider than 2.5 mm.

Apart from difference in maximum size, populations of the two phena resemble each other closely and there is extensive overlap in all characters. It is not possible to subspecifically identify a single individual if it is smaller than 2 mm.

TABLE 1. *Bivariate Statistics of* Hadrotreta primaaea primaaea *from Locality R68/186.* (Measurements in mm; variables as in Fig. 4A, B.)

X	Y	$\bar{X}$	S_x	$\bar{Y}$	S_y	a	b	r	n
				VENTRAL VALVE					
A	D	1.67	0.8353	2.02	1.0639	1.261	−0.081	0.990	25
A	B	1.65	0.8113	0.84	0.4861	0.586	−0.127	0.978	25
A	C	1.79	0.8982	0.68	0.4332	0.463	−0.147	0.960	27
A	F	1.81	0.8894	0.71	0.4796	0.526	−0.236	0.975	28
				DORSAL VALVE					
A	B	2.03	0.8834	1.11	0.5488	0.609	−0.127	0.980	29
A	D	2.07	0.8980	2.45	1.1503	1.267	−0.173	0.989	30
A	E	2.02	0.9123	1.44	0.6859	0.744	−0.061	0.989	26
D	F	2.49	1.1513	1.19	0.6028	0.518	−0.099	0.989	29

[1] In Tables 1-3 the following symbols are used: $\bar{X}$, the arithmetic mean of variable X; S_x, the standard deviation of variable X; $\bar{Y}$, the arithmetic mean of variable Y; S_y, the standard deviation of variable Y; r, the product-moment correlation coefficient; n, the number of pairs of variables; a and b are the coefficients in the regression equation $Y=aX+b$.

There is, however, a significant difference in the population mean of the ratio between the length of the valve to the front of the dorsal median ridge as a fraction of the total length of the valve. In a sample of 44 valves of *H. primaaea primaaea* the mean value of this ratio was 0.673 with a population variance of 0.0566. In contrast, the mean value for a sample of 37 *H. primaaea minor* was 0.627 with a population variance of 0.0586. The two means are significantly different at $P<.001$. Although significant, the difference between the population means is small. Significant differences were not obtained for any other character or ratio. For ventral valves of a comparable size, the apical pits are typically more conspicuous in *H. primaaea primaaea* (cf. Pl. 4, fig. 10 and Pl. 5, fig. 5), but this is a relationship which is difficult to quantify.

Occurrence.—In this study approximately 1,600 specimens were examined from the Combined Metals Member of the Pioche Shale. The principal collections were from localities R68/164 and R68/165 at Pioche Divide, R68/182, R68/185, R68/186, and R68/188 on the northeast slope of Mount Ely, and 70-f-24 near Oak Spring Summit, west of Caliente, Nevada. Details of the collection localities are given in the appendix.

HADROTRETA PRIMAAEA MINOR Rowell, new subspecies

Plate 4, figures 8-12; Plate 5, figures 1,2

Holytype.—KUMIP 115522.

Diagnosis.—Largest individuals of population do not exceed 3 mm in width.

Age.—Pre-*Albertella* Zone, Middle Cambrian.

Discussion.—The distinctions between this form and *H. primaaea primaaea* have been discussed above. Those two phena are treated as chronologic subspecies. In the absence of information about the intervening populations and the existence or lack of morphological gaps between them, the two groups might have been regarded as ecological variants or distinct species. The choice is a compromise.

Occurrence.—Approximately 340 specimens from the Susan Duster Member of the Pioche Shale were collected. The principal collecting localities were R68/167, R68/168, R70/8, R70/9, R70/10, and R70/11, all at Pioche Divide. Details of the collection localities are given in the appendix.

Subfamily LINNARSSONIINAE Rowell, 1965
Genus APHELOTRETA Rowell, new

Etymology.—Greek, *apheles,* even, smooth; *tretos,* perforated.

Type species.—*Aphelotreta minuta* ROWELL, n. sp.

Diagnosis.—Small biconvex Linnarssoniinae with low catacline to moderately apsacline, exteriorly gently concave, ventral pseudointerarea. Apical process not detectable in most individuals, forming low elongate triangular swelling in largest specimens. Dorsal valve with short anacline-orthocline propareas and median plate supported

by median buttress.

Remarks.—Aphelotreta shows greatest resemblance to *Acrothyra* Mathew, which is a contemporary. Adult individuals of the two genera can be readily distinguished because *Acrothyra* has an elongate, bulbous apical process and typically is linguliform in outline. Furthermore, *Aphelotreta* does not possess the long dorsal median ridge that is characteristic of all described species of *Acrothyra.*

In lacking or having a poorly developed apical process, *Aphelotreta* resembles the younger genus *Opisthotreta* Palmer (1955). The two taxa differ in the structure of the ventral posterior sector of the shell. In *Opisthotreta* the ventral pseudointerarea is essentially flat and clearly demarcated from the remainder of the valve by an abrupt flexure of the shell material. Furthermore, in the dorsal valve of *Opisthotreta* the median plate is narrow and pitlike, and a low median ridge extends forward nearly to the front of the valve.

Neotreta Sobolev (1976) from the Upper Cambrian of Khabaravsk also lacks a well-developed apical process, but is unlikely to be confused with *Aphelotreta. Neotreta* is a very tumid genus with wide pseudointerareas in both valves. Available illustrations of the apical region of the ventral valve of *N. tumida,* the type species, suggest that there are differences between the two genera in this region. The extreme ventral apex of *Neotreta* is nipplelike and bears the pedicle foramen (Sobolev, 1976, fig. 1B). In *Aphelotreta* the apical region and protegular structure are like those of *Hadrotreta.* The larval pedicle opening is marginal and the pedicle presumably emerged between the two protegular valves (Pl. 4, fig. 4a).

APHELOTRETA MINUTA Rowell, new species

Figures 7-9; Table 2; Plate 3, figures 1,2, 4,5; Plate 4, figures 1-7

Holotype.—KUMIP 115537.

Diagnosis.—As for genus, which is presently monospecific.

Description.—Shell small, about 15 percent wider than long, maximum width occurring slightly in front of midlength of valve. Subequally biconvex, both valves ornamented only by extremely fine growth lines.

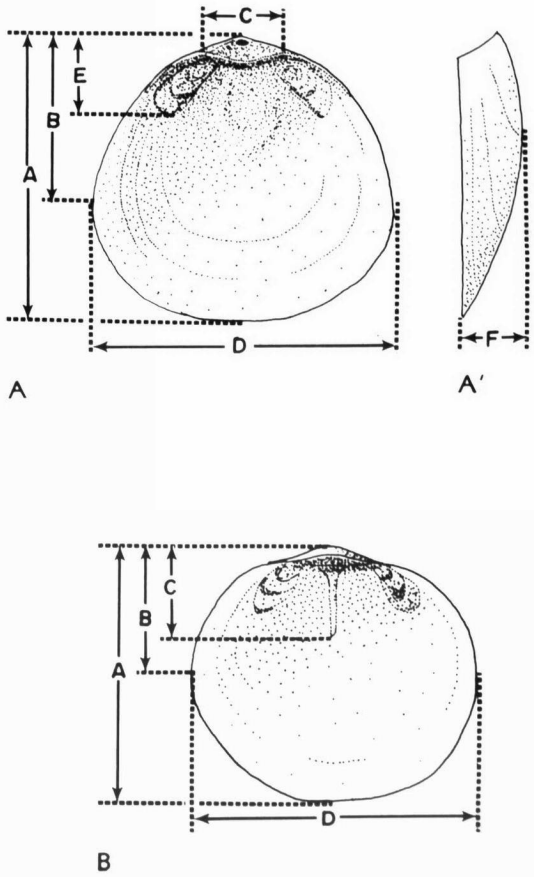

FIG. 7. Diagram of the location of measurements on the ventral valve (A, A′) and the dorsal valve (B) of *Aphelotreta minuta.*

Ventral valve gently convex, maximum height approximately 25 percent of valve length occurring slightly behind midlength of valve. Gently convex in lateral profile, extreme apex slightly incurved over pseudointerarea. Pseudointerarea low, typically slightly apsacline, more rarely catacline or slightly procline. Pseudointerarea commonly gently concave externally, width about 30 percent of maximum width for valve. Intertrough indistinct, external foramen small, notching margin of pitted protegulum. In ventral view, outline subquadrate, posterior margin narrow and nearly straight, posterolateral and anterior margins gently rounded, anterolateral margins strongly curved. Internally almost featureless, internal pedicle foramen slightly larger than external, opening through apex of pseudointerarea, directed anteriorly. Apical pits not im-

pressed, apical process not detectable in most individuals, but apical region slightly thickened between proximal ends of mantle canals. Cardinal muscle scars posteriorly located anterolateral of pseudointerarea, typically extending forward approximately 25 percent of valve length, lightly impressed.

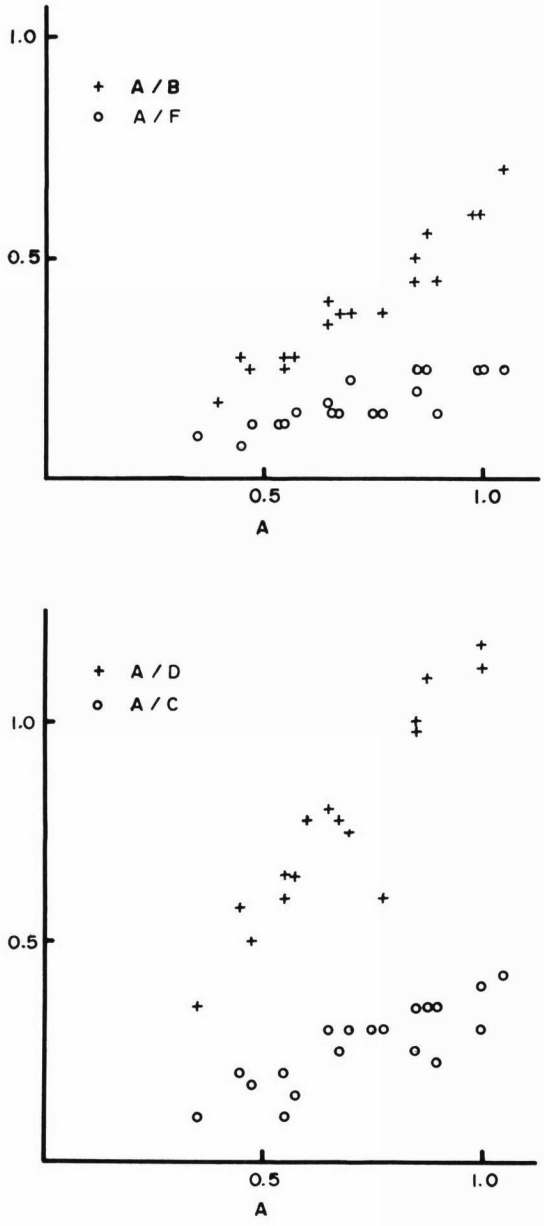

FIG. 8. Scatter diagrams for ventral valves of *Aphelotreta minuta* from locality R68/199. Measurements in mm; variables as indicated in Fig. 7A.

Height of dorsal valve comparable to ventral valve, maximum height occurring just behind midlength of valve. Umbo slightly swollen, incurved and raised above lateral margins of valve. In front of umbo, valve gently and uniformly convex in lateral and anterior profiles. Commissural outline transversely subquadrate to suboval. Internally with short median plate and orthocline to gently anacline propareas. Median plate supported by median buttress that is extended forward as low ridge for about one-third valve length. Rare individuals possess incipient median ridge developed as isolated structure in front of anterior ridgelike extension of median buttress. Cardinal muscle scars elongate oval, extending anterolaterally in front of propareas to about 30 percent of valve length. Other scars not observed.

Age.—Albertella Zone and probably upper part of Pre-*Albertella* Zone, Middle Cambrian. The species is restricted to the upper 90 m of the Pioche Shale. The trilobite fauna of this interval has not yet been examined in detail.

Discussion.—The majority of the specimens are small (Figs. 8, 9) and the largest measurable individual has a length of some 1.15 mm. Given the small size, one is inevitably concerned that the collection may represent juveniles of some better known taxon. As discussed for *Hadrotreta primaaea,* which is a relative giant among acrotretids, internal characters of some species change markedly during ontogeny. Fortunately, however, the external shape typically shows less variation with growth and the form of the juvenile is faithfully reflected by the more proximal growth lines on the shell of a large individual.

Some species of *Acrothyra* show the closest similarity with *Aphelotreta minuta,* but there are consistent differences. When growth lines of a similar size are compared, the ventral outline of those individuals referred to *Acrothyra* is subtriangular; the posterior margin of *A. minuta,* in contrast, is nearly straight and the resulting ventral outline subquadrate. Furthermore, fragments of larger individuals of *A. minuta* occur in the samples. The largest fragment of a ventral valve is probably from an individual some 2.5 mm long, but the apical process of this specimen is still low and subdued, in contrast to the elongate subtriangular projection that characterizes species of *Acrothyra* of a comparable size.

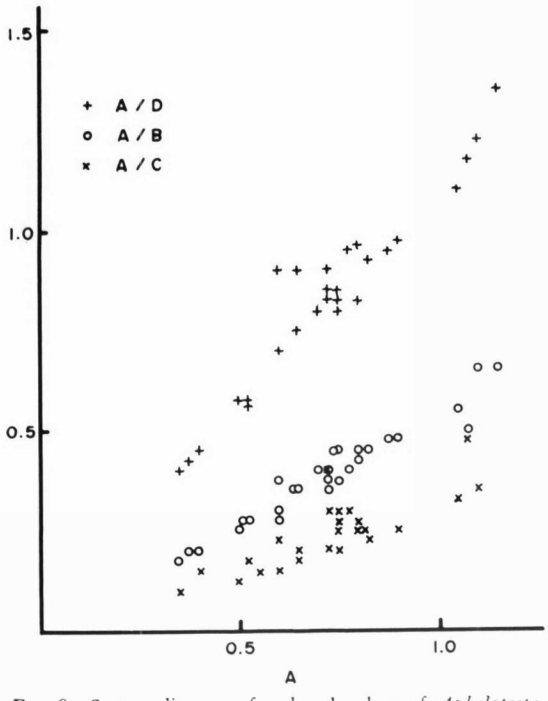

FIG. 9. Scatter diagrams for dorsal valves of *Aphelotreta minuta* from locality R68/199. Measurements in mm; variables as indicated in Fig. 7B.

Aphelotreta minuta appears to differ substantially from any previously described acrotretid.

Occurrence.—The species is known only from the upper part of the A-shale member of the Pioche Shale. Approximately 145 specimens were collected from localities R68/196, R68/199, R68/200, and R68/201 south of Lyndon Gulch on the west side of the Highland Range. Details of collection localities are given in the appendix.

Genus ACROTHYRA Mathew, 1901

Acrothyra MATHEW, 1901, p. 303; WALCOTT, 1912, p. 715; COBBOLD, 1921, p. 348; ROWELL, 1966, p. 26.

Understanding of the morphology of the genus has not improved significantly since Rowell (1966) discussed some of its salient features. More information is available, however, on its local stratigraphic range within the Great Basin. The youngest species is an undescribed form from the basal beds of the *Ptychagnostus gibbus* Zone in the Wheeler Shale of western Utah (McGee, 1978). The oldest species is *A. minor* Walcott, which occurs in the upper 65 m of the A-shale member in the Pioche district.

ACROTHYRA MINOR, Walcott, 1905

Plate 7, figures 4, 6, 8

Acrothyra minor WALCOTT, 1905, p. 303; WALCOTT, 1912, p. 717; RESSER, 1939, p. 22; ROWELL, 1966, p. 28.

Fragments of individuals referred to this species occur abundantly in limestone beds near the middle of the A-shale member. The material is typically abraded and was either washed into the area or subjected to prolonged oscillating currents. Only one ventral valve is complete (Pl. 7, fig. 4) and none of the dorsal valves are undamaged.

The shape of the valves differs little from that of specimens in the type collection (Rowell, 1966), but S.E.M. microscopy allows resolution of detail either previously not detected or seen

TABLE 2. *Bivariate Statistics of* Aphelotreta minuta *from Locality R68/199.* (Measurements in mm; variables as in Fig. 7A, B.)

X	Y	$\bar{X}$	S_x	$\bar{Y}$	S_y	a	b	r	n
				VENTRAL VALVE					
A	D	0.68	0.1870	0.79	0.2229	1.174	–0.019	0.985	16
A	B	0.72	0.2000	0.40	0.1406	0.675	–0.083	0.960	18
A	F	0.72	0.1948	0.18	0.0550	0.243	0.000	0.860	19
D	C	0.79	0.2229	0.25	0.0861	0.337	–0.018	0.873	16
A	E	0.76	0.1718	0.19	0.0469	0.237	0.012	0.868	17
				DORSAL VALVE					
A	D	0.73	0.2027	0.83	0.2257	1.069	0.055	0.960	29
A	B	0.73	0.2027	0.39	0.1172	0.559	–0.016	0.968	29
A	C	0.73	0.1841	0.24	0.0859	0.370	–0.028	0.794	25

only with difficulty. The pedicle foramen notches the posterior margin of the ventral protegulum, like that of *Hadrotreta primaaea*. The apex of the ventral valve, that part lying behind the posterior commissure, is internally thickened and almost plugged by later shell deposits in mature individuals. This thickened region is pierced by the internal continuation of the pedicle opening, which expands slightly in diameter toward the inside of the valve (Pl. 7, fig. 6a). The ventral pseudointerarea is moderately apsacline, and well defined, but is not strongly curved, as it is in some other species of the genus. The characteristic elongate triangular apical process is well displayed by the species. The posterior part of the process is narrow and almost a ridge in old individuals. It is bounded laterally by the mantle canals, which are close together in this part of the valve. The process expands in width anteriorly and increases in height concomitant with the anterolateral divergence of the mantle canals. The dorsal pseudointerarea is buttressed; its median plate is relatively broad and concave, and the propareas are relatively inconspicuous and short (Pl. 7, fig. 8).

Occurrence.—The species is represented by large numbers of broken fragments and some 42 moderately complete valves from the A-shale member. Material was collected from localities R68/197 and R68/200 south of Lyndon Gulch on the west side of the Highland Range. Details of the collection localities are given in the appendix.

Genus and Species Undetermined

Plate 7, figures 3, 7, 9

A rare species occurs in the upper part of the Combined Metals Member some two meters from its top in the Ely Range. This form is known only from three valves in collection R68/187. They are not closely comparable to any described species, but the sample is considered to be inadequate to erect any new taxon. They are most similar to specimens of *Acrothyra,* but lack the linguloid outline characteristic of that genus. Although the apex of the ventral valve is infilled with later shell additions, like that of *A. minor,* there are differences in detail in the form of the apical process. The apical process of the one known ventral valve of the present species is broadly triangular in outline, but its posterior part bears a shallow groove and is not elevated as it is in *Acrothyra.* Less information is available about the dorsal valves. The posterior segments of the major mantle canals are strongly impressed and border the median buttress. The propareas are small, but relatively well developed for a member of the family. More material is required before the phylogenetic affinities of this species can be discussed meaningfully.

Family ACROTHELIDAE Walcott and Schuchert, 1908

Although the acrothelids are known to range from Lower Cambrian into basal Ordovician rocks, they are common only in Middle Cambrian strata. *Acrothele* itself is a cosmopolitan genus and is represented by several species, which are seemingly restricted stratigraphically to the Middle Cambrian. *Orbithele,* whose early species are contemporaneous with later forms of *Acrothele,* also has a wide geographic distribution. It occurs sporadically in upper Middle Cambrian and Upper Cambrian rocks, and is known from Europe (Sdzuy, 1955), Australia (Henderson, 1974), and the western United States. Early Cambrian acrothelids, in contrast, appear to have more restricted geographic distributions. Such genera as *Schizopholis* Waagen, *Spinulothele* Rowell, and *Eothele* are known only from one continent, and they seem to have been endemic forms. It is conceivable that this difference in distribution is an artifact of the data, for Early Cambrian acrothelids are not well known. More probably, the difference is real and reflects a difference in the biology of the animals, in their mode of life, or dispersal mechanisms.

During the past few years considerable attention has been given to the ultrafine surface features of acrotretide protegula (Biernat & Williams, 1970, 1971; Biernat, 1973; Ludvigsen, 1974), but among the Acrothelidae only that of *Orbithele* has been previously examined (Henderson, 1974). Given that adult acrothelids are several times larger than acrotretids, it is perhaps not surprising that their protegulum is correspondingly bigger. Henderson (1974) recorded *Orbithele* protegular sizes ranging from 500 to 620 μm, in contrast to the known range of 90 to 200 μm among acrotretids (Ludvigsen, 1974, p. 141). The pitted surface characteristic of acrotretids is also present in *Orbithele,* but the maxi-

mum pit sizes in *Orbithele* species are larger. Measurements of maximum dimension on 16 of the largest pits of the ventral protegulum of the *Orbithele* sp. figured by Henderson (1974, fig. 1D) average 11 μm. The comparable value for the specimen figured herein of what is probably the same species from the lower Upper Cambrian of western Queensland is 10 μm (Pl. 2, fig. 9a). The protegular ornament of this Australian species of *Orbithele* is similar to that of all Cambrian acrotretids that have been examined. The pits have rounded bases and are separated by ridges and flatter areas, which themselves bear smaller pits (Pl. 2, fig. 9a). It differs from that of the Devonian acrotretid *Opsiconidion* (Ludvigsen, 1974), which has flat-bottomed, overlapping pits. The fine protegular surface fabric of *Orbithele* appears to be characteristic of all the Acrothelidae. In the present study, the protegula of five other species belonging to the family have been examined. The type species of *Acrothele, A. coriacea* Linnarsson, from the Middle Cambrian of Sweden, has basically the same protegular ornament as *Acrothele subsidua* (White) and two other species of the genus from the Middle Cambrian of the Great Basin. A closely comparable ornament is found in *Eothele spurri* (Walcott) from the upper Lower Cambrian of the same region. There is some variation in detail of dimensions and distribution of pits (Pl. 2, figs. 6b, 7b, 9a; Pl. 3, fig. 3b), but the underlying pattern is readily distinguishable. The possible taxonomic usefulness of the protegular surface ornament has not been assessed and further studies are required of its variation within and between populations of one species.

The similarity of acrothelid protegula is not confined to their ornament because all those investigated to date share a comparable gross morphology. The shape of the protegula is relatively complex and differs markedly from that found in any other family of brachiopods. Indeed, the acrothelids are among the few brachiopods that may be confidently identified to family by the protegulum alone. Williams and Rowell (1965, fig. 95) diagrammatically illustrated an acrothelid protegulum, but Henderson's (1974, fig. 1) S.E.M. photographs of *Orbithele* were the earliest to show details of the morphology of these first-formed valves. All acrothelids examined have a relatively large protegulum; the ventral one bears two spines or nodes lying anteriorly and laterally of a median archlike deflection of the shell that bounds the triangular pedicle opening (Pl. 2, fig. 9b; Pl. 3, figs. 3c, 7b). This opening breaches the dorsal margin of the ventral protegulum and in life the pedicle must have emerged between the valves. The dorsal protegulum, which has the same transversely ovate form as the opposing one, carries one or two pairs of spines.

The form and distribution of the protegular spines and nodes are not constant within the family. The Australian early Late Cambrian *Orbithele* has four relatively long dorsal spines that are slender and circular in cross section (Henderson, 1974). The single pair of spines on the ventral protegulum of this species are seemingly shorter, but have a similar cross-sectional shape (Pl. 2, fig. 9b). A presently undescribed species of *Orbithele* from the *"Cedaria"* Zone of Nevada (Pl. 2, fig. 5) has a similar spine configuration, and this may well be a feature that varies little within the genus.

Arrangement of the protegular projections in *Acrothele* differs from that of *Orbithele*. In *Acrothele subsidua* from the Marjum Formation, and in what is subsequently herein called *Acrothele* sp. 1 from the Susan Duster Member of the Pioche Shale, the ventral protegulum bears two low nodes rather than elongate spines (Pl. 2, fig. 8; Pl. 3, fig. 7b). The quality of preservation of the former species eliminates the possibility that one is merely examining spine bases that have lost their spines, because all of the protegulum, including the nodes, is covered by the characteristic pitted ornament. The anterior pair of spines of the dorsal protegula of these two species are also not developed and their position is occupied by a pair of low nodes (Pl. 2, fig. 7a; Pl. 3, fig. 9c). The posterior pair of spines appears to be short and stubby, but in none of the material examined is the extreme apex preserved. The ventral protegular nodes of *Eothele spurri* (Pl. 2, fig. 4) are like those of *Acrothele,* but there are differences on the dorsal protegulum. The posterior pair of dorsal protegular spines of *Eothele* resemble those of *Acrothele;* they are relatively stout and much shorter than those of *Orbithele* (Pl. 1, fig. 1f). The anterior protegular nodes, which occur in *Acrothele,* are almost nonexistent in *Eothele* (Pl. 1, fig. 1f).

Henderson (1974) has interpreted the spines

of *Orbithele* as devices that could have been utilized in helping to right the newly-settled animal if it became inverted. Because of their shortness, or near absence, it is doubtful if the protegular projections of either *Acrothele* or *Eothele* could have been used in this manner. Furthermore, the distribution of the protegular surface ornament over the apices of the spines in *Eothele* (and by analogy in other acrothelids) clearly shows that the spines could not have lengthened with increasing age of the animal. In this respect their growth is unusual; in life they were not deposited by an isolated ring of generative zone budded off from the mantle margin in the manner inferred for siphonotretid spines (Biernat & Williams, 1971). Instead, they must have consisted of nodelike and tubular evaginations of the protegular outer epithelium that were mineralized simultaneously with the remainder of the protegulum.

Genus ACROTHELE Linnarsson, 1876

Acrothele Linnarsson, 1876, p. 20; Walcott, 1912, p. 630; Bell, 1941, p. 219; Cooper, 1952, p. 44; Goryanskij, 1969, p. 63; Pelman, 1977, p. 32.

The genus is represented by abundant but fragmentary material in the Susan Duster Member and is particularly common in the upper one meter of the bed. A few broken specimens have been recovered from the Blue Limestone marker in the A-shale member at Lyndon Gulch. These specimens belong to a second species.

None of the etched material is complete and much of it has lost the outer layer of shell. Fortunately a few incomplete valves from both horizons retain details of ornament and protegular structure. Although specific identification is not possible, there is no doubt of the generic affinity. The material from the Susan Duster Member is of particular interest as it is one of the earliest *Acrothele*.

ACROTHELE sp. 1

Plate 3, figures 6, 7, 9

The gross morphology of material of this species from the Susan Duster Member is comparable with that of most species of the genus, but all of the etched specimens are incomplete fragments of valves. Ventral valves predominate and these consist largely of the thicker, posterior part of the valve.

The ventral pseudointerarea is not strongly demarcated from the adjacent part of the valve, but it is slightly more convex. In a few individuals the apical region of the pseudointerarea bears the fine granular ornament characteristic of the remainder of the postprotegular shell, but in most specimens the pseudointerarea is ornamented only by growth lines. In lateral profile the pseudointerarea is convex; the slope immediately anterior of the beak is concave and becomes flat near the anterior margin of the shell. In posterior profile, the lateral slopes vary between gently concave and flat.

The collections include few specimens of the dorsal valve, but it is seemingly nearly flat or very gently convex and bears a low, broad, median sulcus that arises immediately anterior of the beak. The dorsal beak is slightly inflated above the posterolateral flanks of the valve, and the protegulum is a conspicuous feature (Pl. 3, fig. 9c).

It is probable that this species is the form that Walcott (1908, p. 87) described as *Acrothele subsidua hera*. Walcott had only one specimen of this taxon, a partially exfoliated ventral valve (Pl. 3, fig. 8). The specimen is from USNM locality 31a and the problem with the stratigraphic level of the collection from that locality has already been mentioned in the discussion of *Hadrotreta*. Although Walcott (1908, 1912) considered that the species was of Early Cambrian age, it appears more likely that it came from the Susan Duster Member of Middle Cambrian age. No specimens of *Acrothele* have been found among etched material from lower in the section. Furthermore, the type specimen of *Acrothele subsidua hera* has a few low-amplitude ribs radiating from the beak and confined to the anteromedian sector of the valve. This is an unusual feature in acrothelids, but similar ribs occur on one ventral-valve fragment from the Susan Duster Member (Pl. 3, fig. 6).

Occurrence.—Approximately 70 specimens, all broken, were obtained from the Susan Duster Member at Pioche Divide from localities R68/167, R68/168, R70/7, R70/8, and R70/9. Details of the collection localities are given in the appendix.

ACROTHELE sp. 2

Plate 3, figure 3

A second species of *Acrothele* occurs in the A-shale member in association with abundant *Aphelotreta minuta*. It is represented by only a few fragmentary ventral valves and is specifically indeterminate. If differs from *Acrothele* sp. 1 in its much shorter pedicle foramen (cf. Pl. 3, figs. 3c, 7b). and the pronounced hoodlike extension of the posteromedian sector of the protegulum over the foramen.

Occurrence.—Seven incomplete valves were collected from limestone beds near the middle of the A-shale member from localities R68/199 and R68/201, Lyndon Gulch on the west side of the Highland Range. Details of collection localities are given in the appendix.

Genus EOTHELE Rowell, new

Etymology.—Greek, *eos*, early; *thele*, teat, nipple.

Type species.—*Acrothele spurri* Walcott, 1908, p. 86, pl. 8, figs. 14, 14′, and 14″.

Diagnosis.—Acrothelids with commissure strongly flexed ventrally in posterior quarter of shell. Dorsal beak strongly depressed below posterolateral flanks of valve. Ventral apex in posterior sixth of valve, ventral beak small, conspicuous. Foramen relatively large, elongate suboval slit, ventral of convex pseudointerarea.

Remarks.—*Eothele* possesses a combination of characters not known in any previously described nominal genus. The closest similarity is with *Acrothele*, as Walcott (1908) appreciated. The resemblance between the postprotegular ornament of the two taxa is close and there is near identity in the form of the corresponding protegula of the two genera. Principal differences are in the beak regions of both valves and in the curvature of the commissure. In *Acrothele coriacea*, the type species of *Acrothele*, as in most described species of the genus, the commissure is nearly planar and the dorsal beak is not conspicuous. In contrast, the posterior commissure of *Eothele spurri* is deflected very strongly ventrally and the dorsal beak is consequently depressed below the remainder of the valve (Pl. 1, figs. 1a-c, 1e). The ventral beak of *Eothele* is close to the posterior margin of the valve and is rendered more conspicuous by being strongly procline (Pl. 1, figs. 5, 8).

The relatively elongate foramen of *Eothele* is similar to that of *Schizopholis*, which also has a posteriorly located ventral apex. The two taxa may be readily distinguished by the nearly rectimarginate commissure of *Schizopholis* and the absence of the typical pustulose acrothelid ornament in the latter genus.

EOTHELE SPURRI (Walcott), 1908

Plate 1, figures 1-8; Plate 2, figures 1-4

Acrothele spurri Walcott, 1908, p. 86; Walcott, 1912, p. 656.

Holotype.—USNM 15344a.

Diagnosis.—As for genus, which is presently monospecific.

Description.—Average size for family, maximum length about 6 mm. Shell slightly to moderately oval, width varying between 10 and 30 percent greater than length. Both valves low. Ornament of minute, densely distributed granules (Pl. 1, fig. 1d) and concentric growth lines.

Ventral valve low eccentric cone, apex about 15 percent of valve length in front of posterior margin. In ventral outline lateral margins rounded, anterior margin gently curved to nearly straight, posterior margin gently rounded. Maximum height of valve at apex, height typically 25 to 30 percent of adult valve length. Apex small but prominent, abruptly elevated above adjacent part of valve. Lateral and anterior slopes concave in profile; pseudointerarea convex, strongly procline. External pedicle foramen elongate subtriangular, continued internally as very short subcylindrical tube in adult shell. Other internal features poorly defined, vague indication of pair of large cardinal muscle scars bounded medially by slightly diverging, straplike, bacculate mantle canal impressions.

Dorsal valve gently convex in general form, but surface complex in detail. Beak strongly depressed below lateral margins of valve, posterior part of valve concave in posterior view. Protegulum with one pair of short spines. Internally, pseudointerarea short but wide, width about 60 percent of valve width. Median plate poorly demarcated from propareas, supported by median buttress that expands forward as low, ill-defined median ridge. Vague indication of posterolateral cardinal muscle scars in front of propareas. Other scars not recognizable.

Age.—*Bonnia-Olenellus* Zone, Lower Cam-

brian.

Discussion.—The species is widespread and easily recognized. It is seemingly a useful indicator of the *Bonnia-Olenellus* Zone in shallow-water carbonate units of the Great Basin.

Occurrence.—The study was based on 180 specimens, many of them broken, collected from the Combined Metals Member. Collections were from localities R68/164 and R68/165 at Pioche Divide, R68/181, R68/182, R68/183, R68/185, R68/186, and R68/187 on the northeast slope of Mount Ely, and 70-f-24 near Oak Spring Summit, west of Caliente, Nevada. Details of the collection localities are given in the appendix.

Order PATERINIDA Rowell, 1965

The systematic position of the order Paterinida is enigmatic. The group is typically placed in the Inarticulata because, like most inarticulates, the paterinides have phosphatic shells. In the majority of features, however, the Paterinida are not similar to other inarticulates. Indeed the gross form of their shell is more reminiscent of that of some early orthides. The ventribiconvex shape of paterinides together with their triangular delthyrium and notothyrium is not unlike that of some primitive articulates. Furthermore, the posterior sector of the margin of both valves is straight for some distance lateral of the delthyrium or notothyrium. This linearity suggests that the valves may have opened by rotation about a hinge axis, coincident with the posterior commissure margin, in a manner analogous with that of the articulates. Although the lateral margins of the paterinide delthyrium and notothyrium may be thickened, as Bell (1941) first noted, no teeth or sockets have been recognized in etched material. Bell (1941, p. 213) mechanically prepared a dorsal valve of *Icodonta typica* that showed socketlike structures lateral of the notothyrium. This may be a feature of that species or genus, but it has yet to be confirmed in any other species belonging to the order. However, the general absence of teeth and sockets does not preclude the possibility that the valves opened by rotation. For example, the majority of productidines lack teeth, yet they opened their valves by utilizing the same principle as the remainder of the articulates.

Fortunately, the distribution of muscle scars provides information on the nature of movement between the valves. Functional constraints controlled the distribution of the principal shell muscles. Among typical inarticulates that are free to twist or slide their valves relative to each other, the principal shell muscles are located peripherally within the body cavity. In this position they are able to exert maximum control of the movement of valves that are constrained only by soft tissue. In contrast, the muscles of articulate brachiopods are inserted close to the midline of the shell. There is no mechanical advantage in having laterally placed muscles in valves whose movement is restricted to rotation about a hinge axis.

The musculature of paterinides is not well known, but it is apparent that, like the articulates, their musculature is concentrated near the midline of the body cavity. Bell (1941, p. 213) observed that there is a remote resemblance between the muscle fields of *Icodonta typica* Bell and primitive orthides. Williams and Rowell (1965, p. *H*127) noted that the paterinide muscle field is unlike that of most inarticulates and what appear to be muscle tracks radiate anteriorly and laterally from the beak. One unusually well-preserved specimen of *Dictyonina pannula* shows additional detail of the ventral field (Pl. 8, figs. 2a, b). The muscle field is elongate triangular in outline and is divided by two narrow grooves that are conspicuous anteriorly but fade toward the beak. These two grooves are probably mantle canals. It is tempting, but premature, to homologize the raised area between the grooves with the adductor muscle scars of the Articulata. The raised scars lateral of the mantle canals would be the equivalent of the diductors. The principal difficulty is in interpreting the dorsal musculature. This is less well known, but appears to consist of two pairs of symmetrically arranged, subtriangular thickened areas radiating from the beak; however, no part of the dorsal valve projects behind the inferred hinge axis. Consequently, paterinides could not have employed the lever action used by the majority of the Articulata to open their valves. It is conceivable that they opened their valves like the living terebratulide *Platidia* (Williams & Rowell, 1965, p. *H*27) in which the normal arrangement of the diductor muscles is reversed, the ventral attachment of the diductors being behind the hinge axis, the dorsal attachment be-

ing in front.

At the present time it is not possible to offer a convincing functional interpretation of paterinide shell musculature. It is clear, however, that the distribution of muscle scars is radically different from that of other inarticulate brachiopods. This distinction, coupled with the unique features associated with the pedicle opening, suggests that the paterinides may not have close phylogenetic relationship with the remaining members of the class Inarticulata.

Superfamily PATERINACEA Schuchert, 1893
Family PATERINIDAE Schuchert, 1893
Genus DICTYONINA Cooper, 1942

Dictyonina Cooper, 1942, p. 228; Cooper, 1952, p. 40.

The genus is a typical paterinid in its external form and is characterized by having a delicate microornament of honeycomblike depressions bounded by narrow raised ridges. The homeodeltidium is commonly absent, and is never well developed, a feature which, together with absence of ridges on the protegula, serves to distinguish *Dictyonina* from the Ordovician genus *Dictyonites* Cooper.

DICTYONINA PANNULA (White), 1874

Figures 10-12; Table 3; Plate 7, figures 1,2; Plate 8, figures 1-5

Trematis pannulus White, 1874, p. 6.

Micromitra (*Iphidella*) *pannula* Walcott, 1912, p. 361 (see for early synonymy).

Dictyonina pannula Cooper, 1942, p. 228; Mount, 1974, p. 1.

Holotype.—USNM 15331a.

Diagnosis.—Protegulum of both valves inconspicuous; homeodeltidium absent or limited to apex of delthyrium, homeochilidium lacking; ventral valve apsacline, rarely catacline; microornament on mature part of shell formed by short curved ridges bounding diamond-shaped, shallow pits.

Description.—Ventribiconvex shells, transversely oval in commissural outline. Shell material thin, ornamented by variably developed concentric growth lines and microornament of shallow pits. Pits tending to be arranged in rows radiating from beak, pits in each row staggered relative to each other, bounded by low curved ridges (Pl. 8, fig. 5b) that give pits in

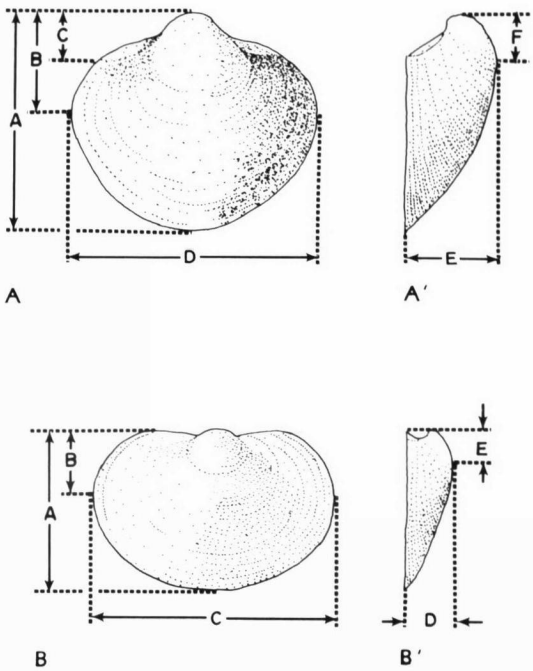

Fig. 10. Diagram of the location of measurements on the ventral valve (A, A′) and the dorsal valve (B, B′) of *Dictyonina pannula.*

mature part of shell a subdiamond-shaped outline.

Width of ventral valve about 15 percent greater than length, maximum width occurring about 35 percent of valve length in front of beak. Lateral and anterior margins gently rounded, posterior commissural margin nearly straight. Valve typically apsacline, beak gently incurved over delthyrium. Maximum height about 35 percent of valve length, occurring about 20 percent of valve length in front of beak. Delthyrium with apical angle of 80 to 90°, typically open; lateral margins commonly unmodified, slightly thickened in a few large individuals (Pl. 8, fig. 2a), thickening extending across apex of delthyrium producing a pedicle callist. Propareas rarely evident, narrow in large individuals.

Dorsal valve transversely oval, posterior margin nearly straight, maximum width about 40 percent greater than length, occurring about 35 percent of valve length in front of beak. Gently convex, maximum height about 25 percent of length, developed slightly in front of beak. Notothyrium open, apical angle about 130°, lateral margins not thickened, propareas absent or poorly developed in large individuals.

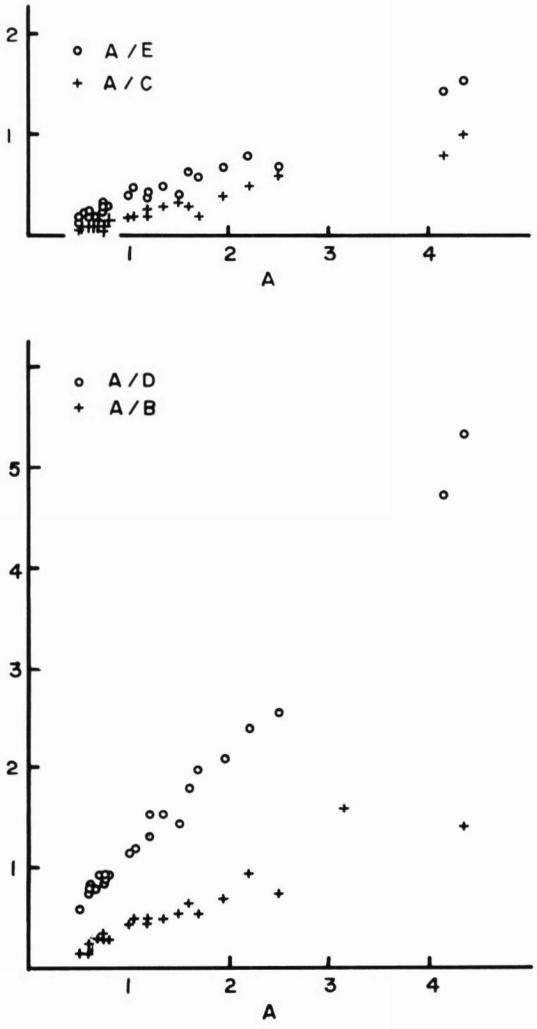

FIG. 11. Scatter diagrams for ventral valves of *Dictyonina pannula* from locality R68/188. Measurements in mm; variables as indicated in Fig. 10A.

Age.—Upper *Bonnia-Olenellus* to Pre-*Albertella* zones.

Discussion.—*Dictyonina pannula* is the type species of the genus. The holotype is a poorly preserved dorsal valve [USNM 15331a] that fortunately retains a small part of the original shell with its characteristic ornament. The precise stratigraphic level from which the holotype came is unknown. It was collected in the Pioche district and the present study shows that only one species of *Dictyonina* occurs in upper Lower and lower Middle Cambrian rocks of that area. Virtually by default this species is regarded as *Dictyonina pannula*.

The pitted microornament shows considerable variability in its development both between different specimens and between different parts of the same valve. The ornament is shallow and consequently is readily effaced by abrasion or diagenetic effects. Some of the variation, however, is not secondary. In a few valves the pitted mi-

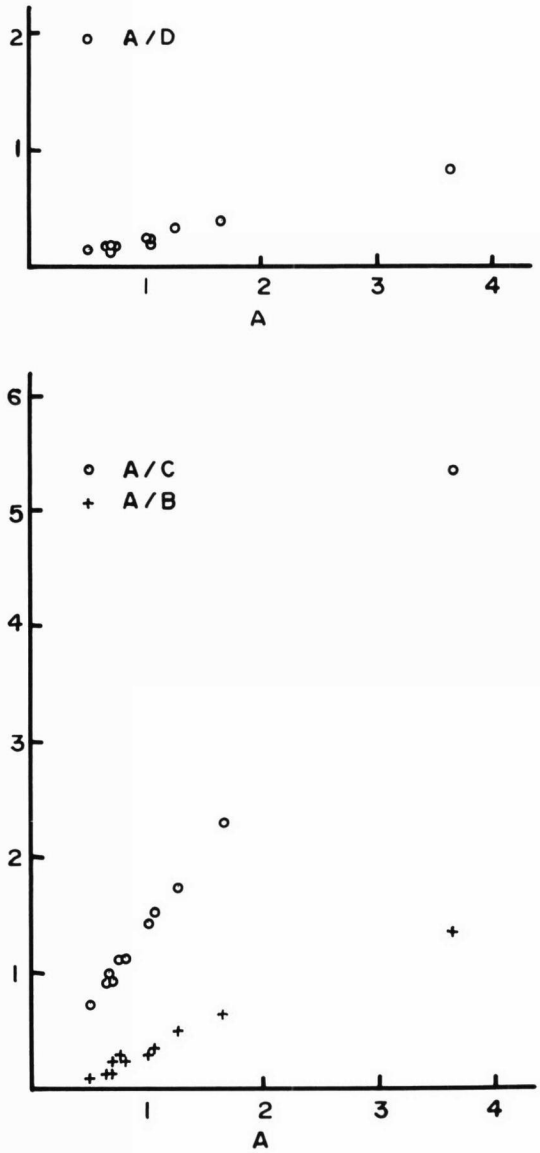

FIG. 12. Scatter diagrams for dorsal valves of *Dictyonina pannula* from locality R68/188. Measurements in mm; variables as indicated in Fig. 10B.

TABLE 3. *Bivariate Statistics of* Dictyonina pannula *from Locality R68/188.*
(Measurements in mm; variables as in Fig. 10A, B.)

X	Y	$\bar{X}$	S_x	$\bar{Y}$	S_y	a	b	r	n
				VENTRAL VALVE					
A	D	1.41	1.0303	1.63	1.1853	1.142	0.024	0.993	23
A	B	1.41	1.0303	0.53	0.3510	0.335	0.055	0.982	23
A	C	1.41	1.0303	0.28	0.2377	0.226	–0.043	0.981	23
A	E	1.41	1.0303	0.50	0.3542	0.339	0.022	0.987	23
A	F	1.41	1.0303	0.32	0.1840	0.152	0.106	0.851	23
				DORSAL VALVE					
A	C	1.15	0.8501	1.66	1.2415	1.459	1.242	0.999	11
A	B	1.15	0.8501	0.40	0.3381	0.394	–0.058	0.991	11
A	D	1.18	0.8840	0.29	0.2035	0.228	0.020	0.991	10
A	E	1.18	0.8840	0.29	0.1786	0.189	0.066	0.936	10

croornament is replaced by a band of strong concentric growth lines (Pl. 8, fig. 4). The growth lines may persist to the periphery of the valve or may, in turn, be replaced marginally by the usual microornament.

Occurrence.—Approximately 400 valves were obtained from collections of the Combined Metals and Susan Duster members. The principal collecting localities were: a) from the Combined Metals Member localities R68/164 and R68/165 at Pioche Divide, R68/180, R68/181, R68/182, R68/183, R68/185, R68/186, and R68/188 on the northeast slope of Mount Ely, 70-f-24 near Oak Spring Summit, west of Caliente, Nevada; and b) from the Susan Duster Member localities R68/167, R68/168, R70/9, R70/10, and R70/11 at Pioche Divide. Details of the collection localities are given in the appendix.

Genus MICROMITRA Meek, 1873

Micromitra MEEK, 1873, p. 479.

Fragments of a thick-shelled paterinide with well-developed homeodeltidium occur sporadically in the limestone residues of the A-shale member (Fig. 2). The material is too broken to merit description and it is not possible to be certain whether it represents one, or more than one, species.

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APPENDIX

Collection Localities
(All localities are in Nevada unless otherwise indicated.)

Locality no.	Description
R60/1	Limestone in Middle Cambrian shales, Kinnekulle, Sweden. 13°23′ E., 58°37′ N.
R68/164	Combined Metals Member, 5 m below top, Pioche Shale, Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R68/165	Combined Metals Member, 2 m below top, Pioche Shale, Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R68/167	Susan Duster Member, 1.3 m above base, Pioche Shale, outcrop above road at Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R68/168	Susan Duster Member, top 30 cm of member, Pioche Shale, outcrop above road at Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R68/180	Combined Metals Member, 12.3 m below top, Pioche Shale, northeast slope of Mount Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/181	Combined Metals Member, 11.1 m below top, Pioche Shale, northeast slope of Mount Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/182	Combined Metals Member, 10.2 m below top, Pioche Shale, northeast slope of Mount Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/183	Combined Metals Member, 7.7 m below top, Pioche Shale, northeast slope of Mount Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/185	Combined Metals Member, 4.9 m below top, Pioche Shale, northeast slope of Mount Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/186	Combined Metals Member, 2.8 m below top, Pioche Shale, northeast slope of Mount Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/187	Combined Metals Member, 1.8 m below top, Pioche Shale, northeast slope of Mt. Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/188	Combined Metals Member, 0.9 m below top, Pioche Shale, northeast slope of Mt. Ely, Lincoln County; SE¼SW¼ sec. 16, T. 1 N., R. 67 E.
R68/196	A-shale member, 29.2 m below top, Pioche Shale, on spur 400 m south of Lyndon Gulch, west side of Highland Range, Lincoln County; sec. 9 (unsurveyed), T. 1 S., R. 66 E.
R68/197	A-shale member, 42 m below top, Pioche Shale, on spur 400 m south of Lyndon Gulch, west side of Highland Range, Lincoln County; sec. 9 (unsurveyed), T. 1 S., R. 66 E.
R68/199	A-shale member, 62 m below top, Pioche Shale, on spur 400 m south of Lyndon Gulch, west side of Highland Range, Lincoln County; sec. 9 (unsurveyed), T. 1 S., R. 66 E.
R68/200	A-shale member, 66.1 m below top, Pioche Shale, on spur 400 m south of Lyndon Gulch, west side of Highland Range, Lincoln County; sec. 9 (unsurveyed), T. 1 S., R. 66 E.
R68/201	A-shale member, 84.3 m below top, Pioche Shale, on spur 400 m south of Lyndon Gulch, west side of Highland Range, Lincoln County; sec. 9 (unsurveyed), T. 1 S., R. 66 E.
R70/7	Susan Duster Member, 0.1 m below top, Pioche Shale, outcrop above road at Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R70/8	Susan Duster Member, 0.2 m below top, Pioche Shale, outcrop above road at Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R70/9	Susan Duster Member, 0.6 m below top, Pioche Shale, outcrop above road at Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R70/10	Susan Duster Member, 1.7 m below top, Pioche Shale, outcrop above road at Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R70/11	Susan Duster Member, 1.8 m below top, Pioche Shale, outcrop above road at Pioche Divide, Lincoln County; SW¼NE¼ sec. 27, T. 1 N., R. 67 E.
R73/27B	Lincoln Peak Formation, about 60 m above the base of the Upper Cambrian, south bank Cleve Creek, White Pine County; NW¼ sec. 29 (unsurveyed), T. 16 N., R. 66 E.
26-M-254	Marjum Formation, 78 m above base, west side of low ridge, 1,200 m due north of original Antelope Spring, House Range, Utah; NW¼NE¼ sec. 2, T. 17 S., R. 13 W.
70-f-24	Upper 7 m of nodular limestone above ledge-forming part of Combined Metals Member, Pioche Shale; north of Highway 93, west of Oak Spring Summit, Lincoln County; sec. 8, T. 4 S., R. 65 E.

Locality no.	Description
USNM 31a	"Lower Cambrian: Limestone and interbedded siliceous shales of the Pioche Formation [Walcott, 1908a, p. 11], just above the quartzite on the east side of the anticline, near Pioche, Lincoln County, Nev. (C. D. Walcott and J. E. W., 1885)." Walcott, 1912, p. 192.
L172	Mungerebar Limestone, Lower Mindyallan, 16 km ENE of McCabe Knob, Mungerebar, Dajarra district, western Queensland, Australia; 22°17′ S., 138°58′30″ E.

EXPLANATION OF PLATES

PLATE 1

FIGURE

1-8. *Eothele spurri* (Walcott).——*1a-f.* Dorsal valve, exterior; *a,b,* stereogram, ×17; *c,* oblique lateral view, ×17; *d,* detail of ornament of anterolateral region of valve, ×125; *e,* oblique posterior view showing strong deflection of commissure, ×17; *f,* detail of dorsal protegulum showing pitted ornament over apex of spine, ×125; all KUMIP 115531, locality 70-f-24.——*2a,b.* Dorsal valve, interior; *a,b,* stereogram, ×17; KUMIP 115530, locality 70-f-24.——*3a,b.* Holotype; *a,b,* lateral and external views of exfoliated ventral valve, ×4; USNM 15344a, locality USNM 31a.——*4a-c.* Juvenile ventral valve; *a,b,* stereogram, ×16; *c,* detail of protegular ornament, ×650; KUMIP 115528, locality 70-f-24.——*5a,b.* Well-preserved ventral valve; *a,b,* stereogram, ×6; KUMIP 115529, locality 70-f-24.——*6.* Paratype; exfoliated ventral valve, ×4; USNM 15344b, locality USNM 31a.——*7a,b.* Dorsal valve; *a,* interior showing pseudointerarea; *b,* exterior, ×8; KUMIP 115509, locality R68/164.——*8.* Ventral valve; exterior of large specimen, ×6; KUMIP 115508, locality R68/164.

PLATE 2

FIGURE

1-4. *Eothele spurri* (Walcott); all specimens from locality 70-f-24.——*1a-c.* Dorsal valve; *a,* detail of median plate and buttress, ×65; *b,* posterior oblique view showing ventral deflection of commissure, ×18; *c,* oblique lateral view of interior showing median ridge, ×18; KUMIP 115530. ——*2.* Dorsal valve, detail of apex of protegular spine, ×330; KUMIP 115531.——*3a,b.* Ventral valve; *a,* posterior, and *b,* lateral views showing detail of foramen and pseudointerarea, ×10; KUMIP 115527.——*4.* Juvenile ventral valve, protegulum and detail of pedicle foramen, ×60; KUMIP 115528.

5. *Orbithele* sp. Detail of protegulum of poorly preserved dorsal valve, ×60; KUMIP 115475, locality R73/27B.

6. *Acrothele coriacea* Linnarsson.——*6a,b.* Dorsal valve; *a,* protegulum with four low, nodelike spines, ×130; *b,* detail of protegular ornament, ×700; KUMIP 115473, locality R60/1.

7-8. *Acrothele subsidua* (White); all locality 26-M-254.——*7a-c.* Dorsal valve; *a,* oblique posterior view of protegulum showing two anterior nodes and two short spines, ×65; *b,* detail of protegular ornament, ×700; *c,* exterior view, ×14; KUMIP 115478.——*8.* Oblique posterior view of ventral protegulum showing two low nodes, ×55; KUMIP 115479.

9. *Orbithele* sp.——*9a,b.* Ventral protegulum; *a,* detail of protegular ornament, ×700; *b,* detail of protegulum showing foramen and two slender spines, ×70; KUMIP 115474, locality L172.

PLATE 3

FIGURE

1,2,4,5. *Aphelotreta minuta* Rowell, n. gen. and sp.; all from locality R68/199.——*1a,b.* Ventral valve interior; *a,b,* stereogram, ×33; KUMIP 115469. ——*2a,b.* Ventral valve exterior; *a,b,* stereogram, ×33; KUMIP 115472.——*4a,b.* Dorsal valve interior; *a,b,* stereogram, ×33; KUMIP 115471. ——*5.* Dorsal valve interior with well-developed median ridge, ×33; KUMIP 115470.

3. *Acrothele* sp. 2.——*3a-c.* Ventral valve; *a,* fragment, oblique posterior view, ×18; *b,* detail of protegular ornament, ×1,300; *c,* shape of pedicle foramen and relation to protegulum, ×60; KUMIP 115534, locality R68/199.

6,7,9. *Acrothele* sp. 1; all from locality R68/168.——*6.* Oblique view of ventral valve fragment showing radial ornament on anterior slope, ×10; KUMIP 115538.——*7a,b.* Ventral valve fragment; *a,* oblique posterior view, ×10; *b,* detail of pedicle foramen, ×70; KUMIP 115477.——*9a-c.* Incomplete dorsal valve; *a,* exterior, ×16; *b,* detail of ornament on anterior part of valve, ×140; *c,* posterior view showing protegulum, ×32; KUMIP 115476.

8. *Acrothele subsidua hera* Walcott. Holotype, ventral valve, largely exfoliated, ×7; USNM 52024a, locality USNM 31a.

PLATE 4

FIGURE

1-7. *Aphelotreta minuta* Rowell, n. gen. and sp.; all from locality R68/199.——*1.* Detail of dorsal pseudointerarea and median buttress, ×125; KUMIP 115470.——*2a,b.* Ventral valve; *a,* oblique posterior and *b,* oblique lateral views, ×33; KUMIP 115472.——*3.* Holotype, ventral valve interior, ×33; KUMIP 115537.——*4a,b.* Ventral valve; *a,* protegulum, ×150; *b,* protegular ornament, ×3,200; KUMIP 115510.——*5.* Oblique lateral view of dorsal valve, ×33; KUMIP 115571.——*6.* Ventral valve, oblique interior showing lack of apical process, ×33; KUMIP 115469.——*7a,b.* Dorsal valve, exterior; *a,b,* stereogram, ×33; KUMIP 115511.

8-12. *Hadrotreta primaaea minor* Rowell, n. subsp.——*8a-d.* Dorsal valve, interior; *a,* detail of pseudointerarea and median buttress, ×70; *b,* oblique lateral view, ×22; *c,d,* stereogram, ×22; KUMIP 115521, locality R68/168.——*9.* Ventral valve, interior, ×22; KUMIP 115517A, locality R70/11.——*10a,b.* Holotype, ventral valve interior; *a,b,* stereogram, ×22; KUMIP 115522, locality R68/168.——*11.* Both valves, posterior view, ×33; KUMIP 115519, locality R70/11.——*12.* Dorsal valve, interior view, ×35; KUMIP 115520, locality R68/168.

PLATE 5

FIGURE

1-2. *Hadrotreta primaaea minor* Rowell, n. subsp.——

1a,b. Ventral valve exterior; *a,b,* stereogram, ×20; KUMIP 115518, locality R70/11.——*2a,b.* Dorsal valve exterior; *a,b,* stereogram, ×18; KUMIP 115523, locality R68/168.

3-10. *Hadrotreta primaaea primaaea* Walcott; all from locality R68/186.——*3a,b.* Dorsal valve; *a,* oblique posterior view, ×16; *b,* exterior view, ×16; KUMIP 115466.——*4a-c.* Large ventral valve, interior; *a,b,* stereogram, ×9; *c,* detail of internal pedicle opening and apical pits, ×80; KUMIP 115513.——*5a,b.* Small ventral valve, interior; *a,b,* stereogram, ×16; KUMIP 115468. ——*6a,b.* Relatively elongate, large dorsal valve, interior; *a,b,* stereogram, ×9; KUMIP 115525. ——*7a,b.* Ventral valve exterior; *a,b,* stereogram, ×16, KUMIP 115465.——*8a,b.* Small dorsal valve, interior; *a,b,* stereogram, ×16; KUMIP 115467.——*9.* Interior detail of posterior region of large dorsal valve, ×14; KUMIP 115512.——*10.* Relatively broad, large dorsal valve, interior, ×9; KUMIP 115526.

PLATE 6

FIGURE

1-9. *Hadrotreta primaaea primaaea* (Walcott); all from locality R68/186.——*1a-c.* Juvenile ventral valve; *a,* exterior view, ×35; *b,* oblique posterior view, ×35; *c,* detail of pitted protegular ornament, ×700; KUMIP 115464.——*2a-c.* Juvenile ventral valve; *a,* oblique posterior view, ×35; *b,* exterior view, ×30; *c,* detail of pedicle foramen and apical part of intertrough, ×250; KUMIP 115463.——*3.* Oblique interior view of small ventral valve showing early stage of apical process, ×16; KUMIP 115468.——*4a-c.* Very small ventral valve; *a,* lateral view, ×60; *b,* oblique posterior view, ×60; *c,* detail of pedicle foramen posteriorly located on protegulum, ×600; KUMIP 115462.——*5.* Oblique interior view of juvenile dorsal valve with fused median septum and buttress, ×16; KUMIP 115467.——*6.* Oblique posterior view of juvenile ventral valve with well-developed intertrough, ×16; KUMIP 115465. ——*7.* Posterior view of large ventral valve, ×8; KUMIP 115515.——*8.* Interior view of large dorsal valve with well-developed muscle scars, ×8; KUMIP 115512.——*9a-c.* Both valves; *a,* posterior view with detail of pedicile foramen, ×250; *b,* ventral view, ×65; *c,* detail of ornament of right anterior of ventral valve, ×1,200; KUMIP 115461.

PLATE 7

FIGURE

1,2,5. *Dictyonina pannula* (White).——*1a-c.* Ventral valve, exterior; *a,b,* stereogram, ×6; *c,* posterior view with well-developed delthyrium, ×8; 115545, locality R68/188.——*2a,b.* Dorsal view of both valves; *a,b,* stereogram, ×6; KUMIP 115544, locality R68/188.——*5.* Exterior of dorsal valve, ×6; USNM 15332a, locality USNM 31a.

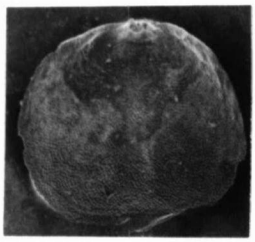
3,7,9. Linnarssoniinae, genus and species undetermined; all from locality R68/187.——*3a-c.* Incomplete ventral valve interior; *a,b,* stereogram showing elongate apical process, ×16; *c,* slightly oblique view showing shallow groove on process, ×20; KUMIP 115500.——*7.* Fragment of dorsal valve, interior view, ×30; KUMIP 115498.——*9.* Fragment of dorsal valve, interior view, ×30; KUMIP 115499.

4,6,8 *Acrothyra minor* Walcott.——*4a,b.* Ventral valve interior; *a,b,* stereogram, ×14; KUMIP 115539, locality R68/197.——*6a,b.* Ventral valve fragment; *a,* interior, with well-developed apical process, ×20; *b,* exterior, detail of posterior of valve, ×65; KUMIP 115496, locality R68/199.——*8a,b.* Incomplete dorsal valve; *a,* interior, ×17; *b,* oblique lateral view of interior, ×20; KUMIP 115497, locality R68/199.

PLATE 8

FIGURE

1-5. *Dictyonina pannula* (White).——*1a,b.* Small ventral valve; *a,* oblique lateral view, ×25; *b,* exterior view, ×25; KUMIP 115456, locality R68/188.——*2a,b.* Ventral valve; *a,* oblique interior view, ×10; *b,* interior view, ×10; both showing well-developed muscle scars and mantle canals; KUMIP 115543, locality 70-f-24.——*3a,b.* Oblique posterior view of complete shell, ventral apex damaged; *a,b,* stereogram, ×8; KUMIP 115544, locality R68/188.——*4.* Oblique view of ornament of dorsal valve, honeycomb microornament interrupted by growth lines, ×50; KUMIP 115454, locality R68/188.——*5a,b.* Damaged dorsal valve; *a,* whole specimen, showing well-developed microornament, ×30; *b,* detail of ornament on anterior part of valve, ×280; KUMIP 115458, locality 70-f-24.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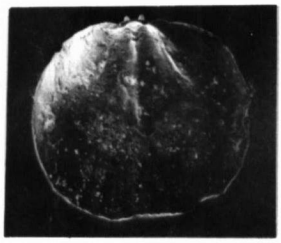
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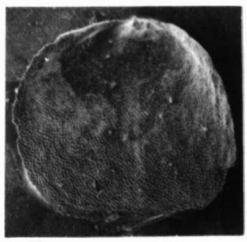
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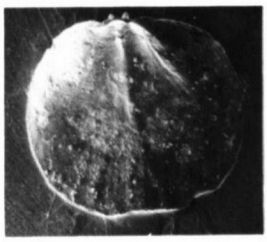
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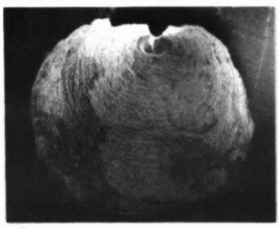
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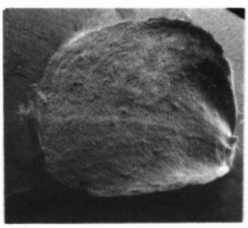
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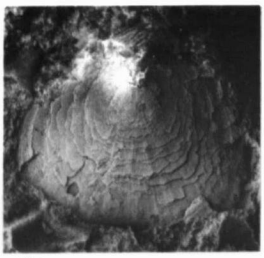
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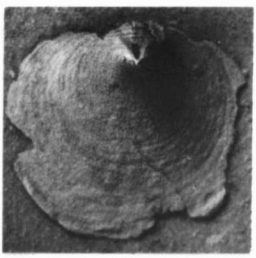
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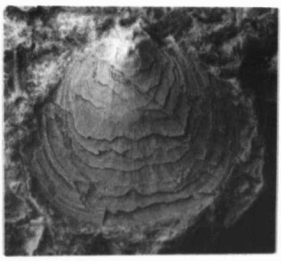
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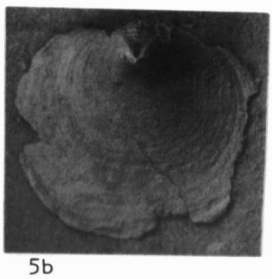
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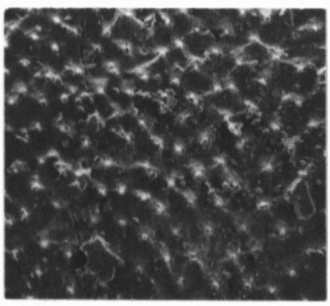
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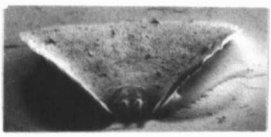
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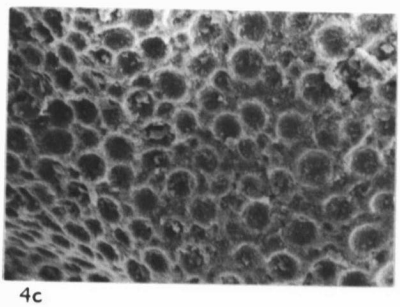
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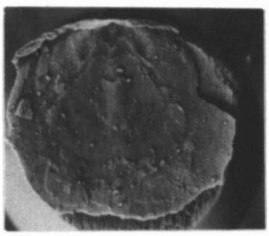
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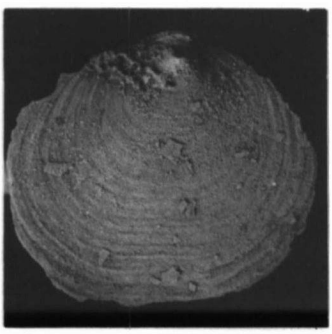
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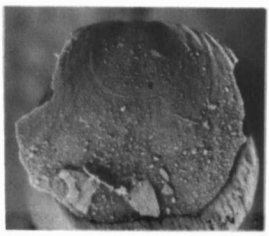
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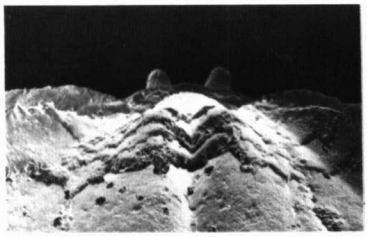
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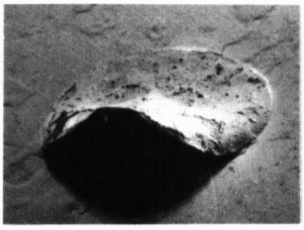
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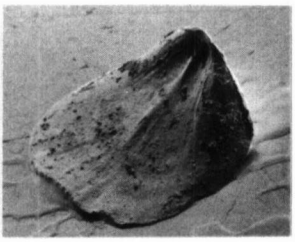
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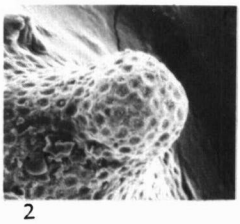
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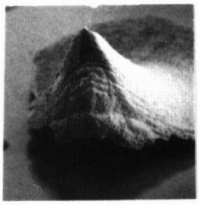
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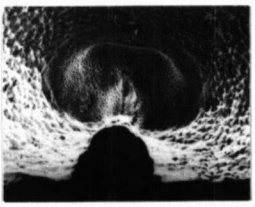
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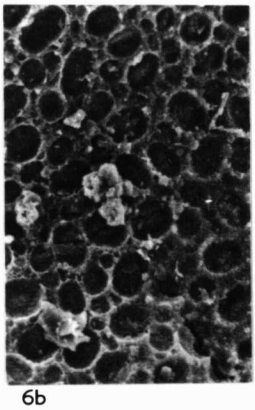
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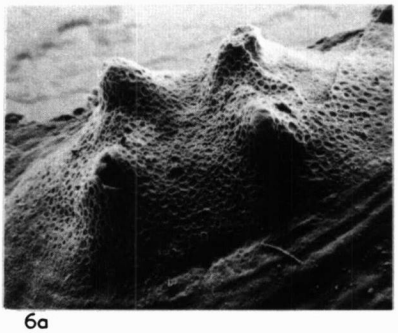
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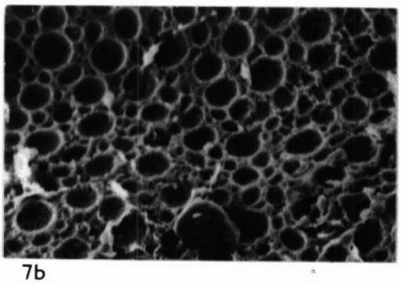
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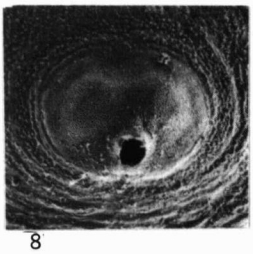
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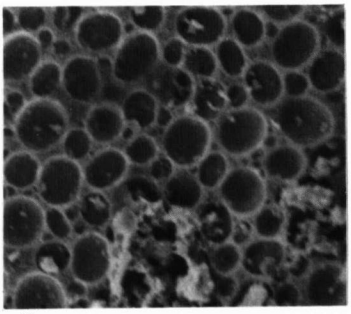
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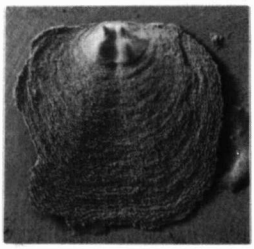
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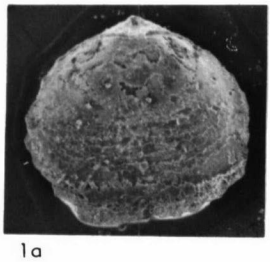
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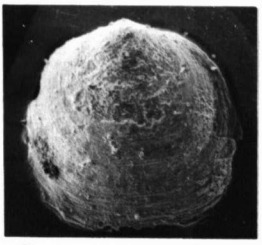
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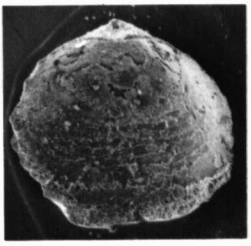
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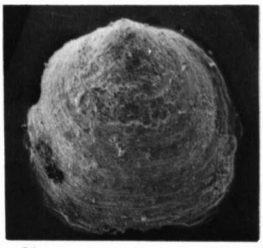
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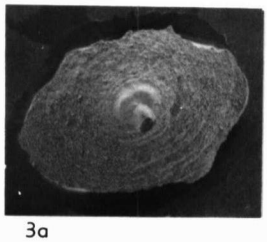
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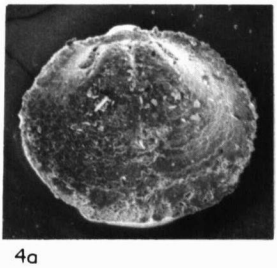
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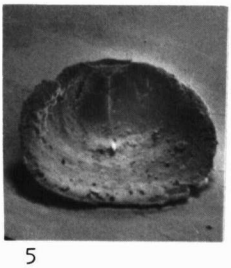
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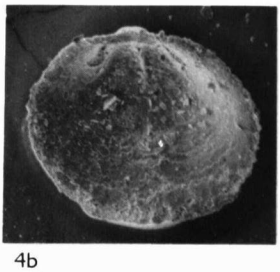
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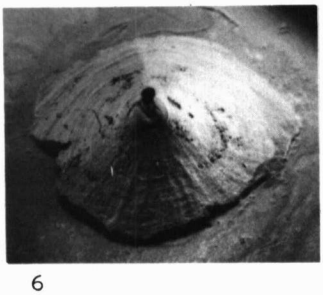
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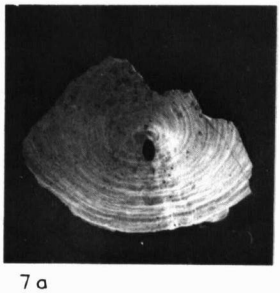
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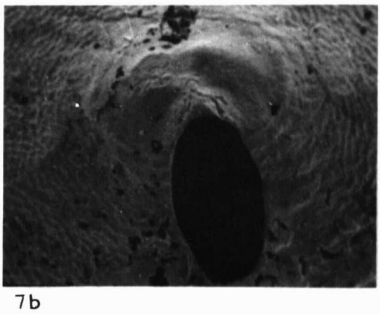
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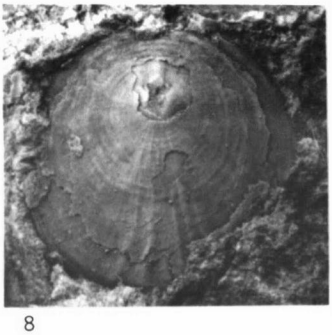
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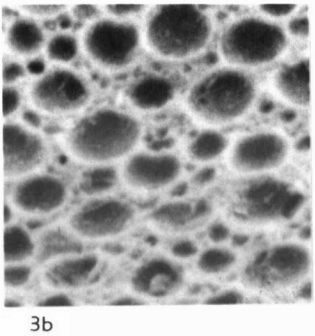
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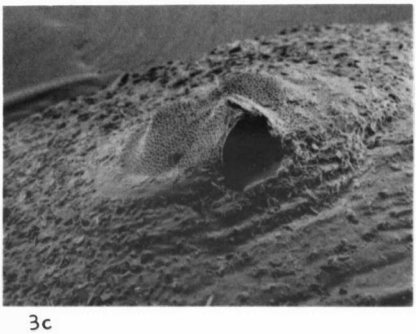
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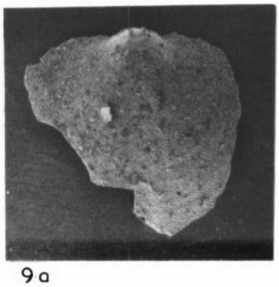
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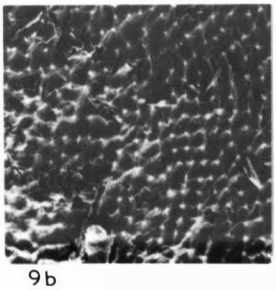
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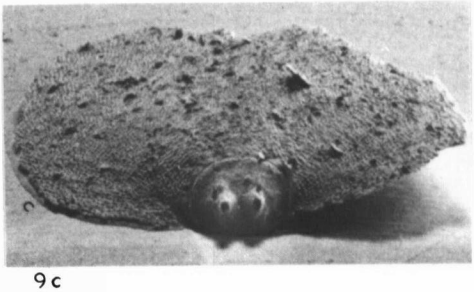
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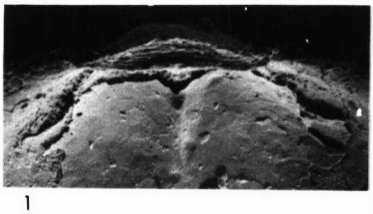
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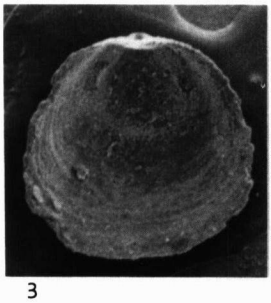
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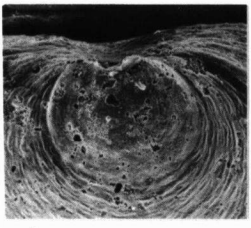
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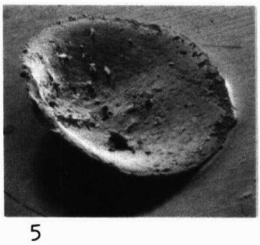
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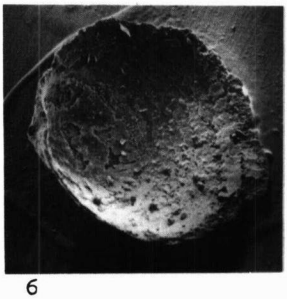
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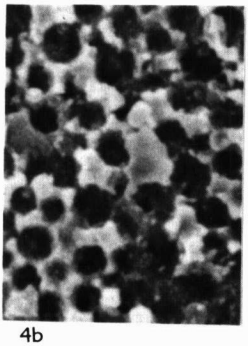
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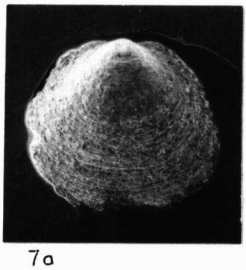
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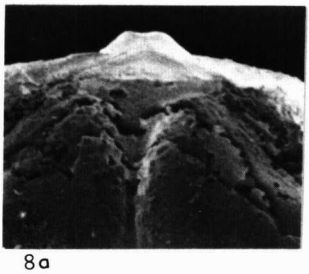
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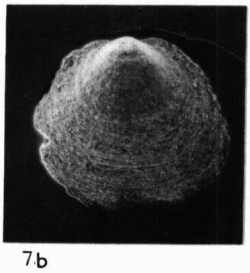
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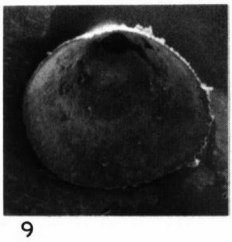
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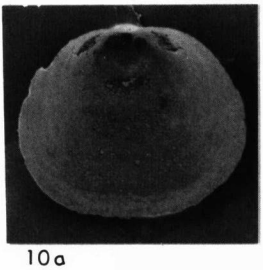
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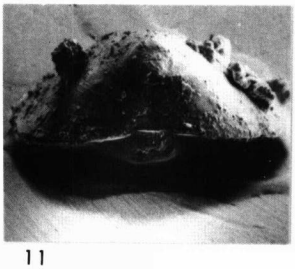
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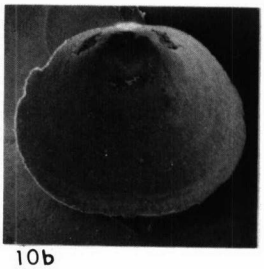
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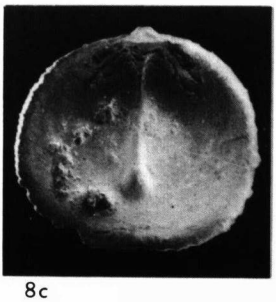
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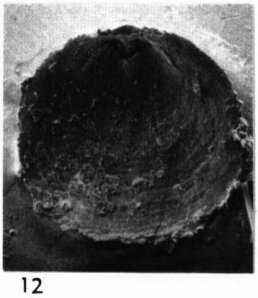
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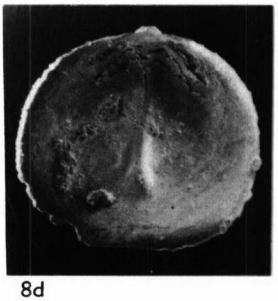
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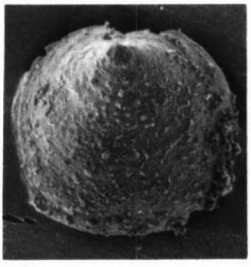
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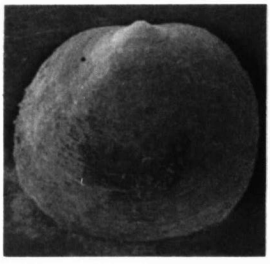
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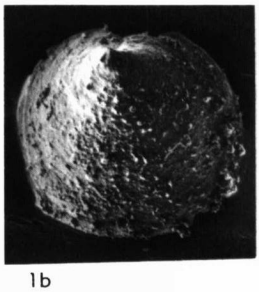
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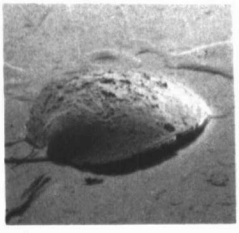
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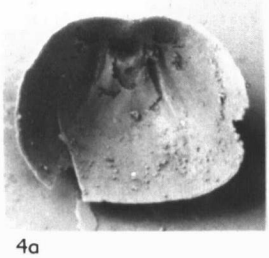
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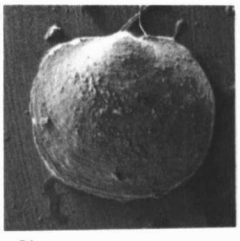
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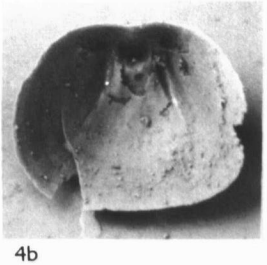
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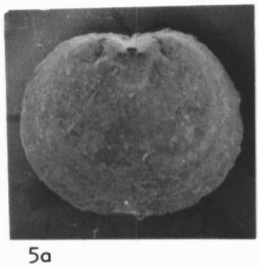
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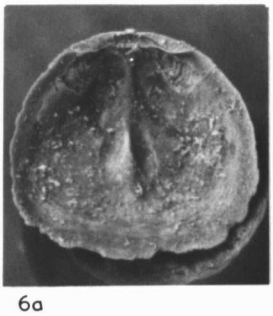
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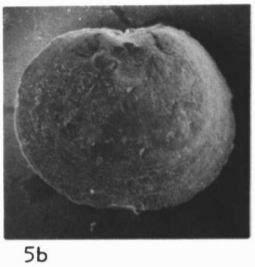
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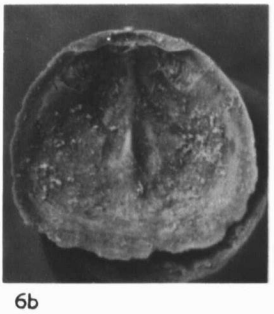
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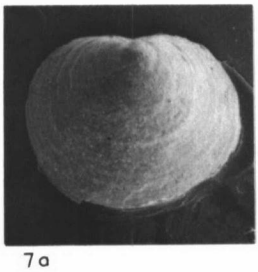
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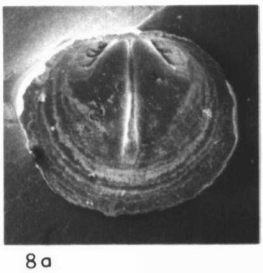
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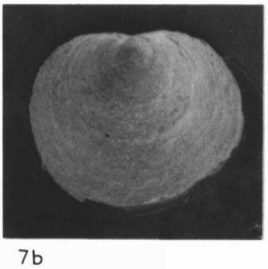
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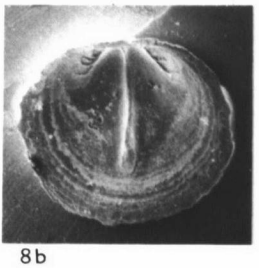
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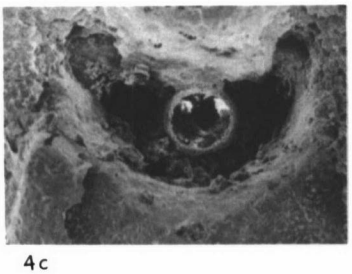
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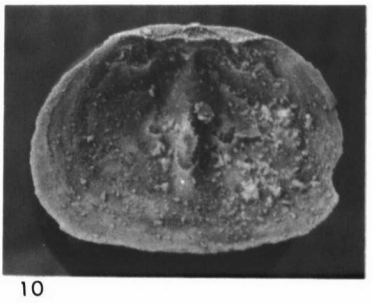
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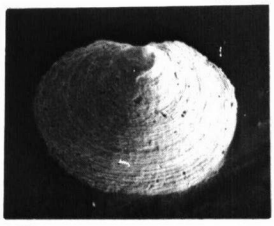
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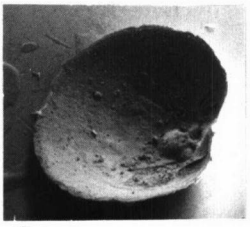
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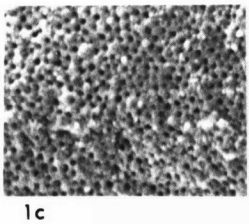
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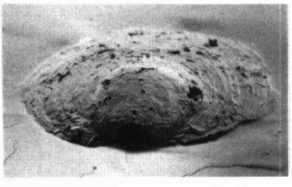
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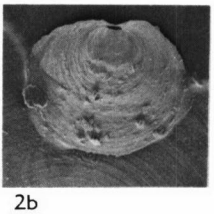
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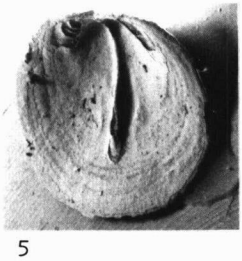
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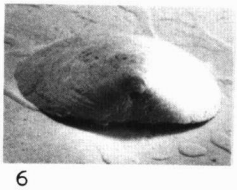
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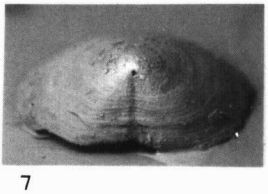
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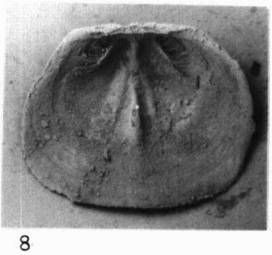
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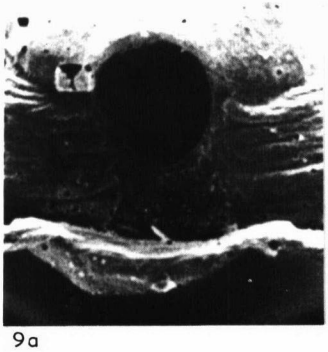
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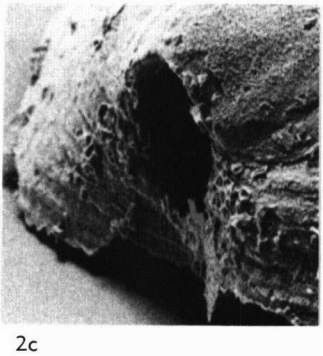
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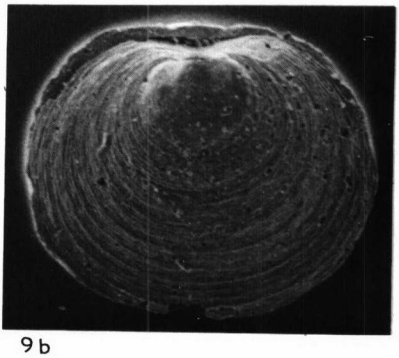
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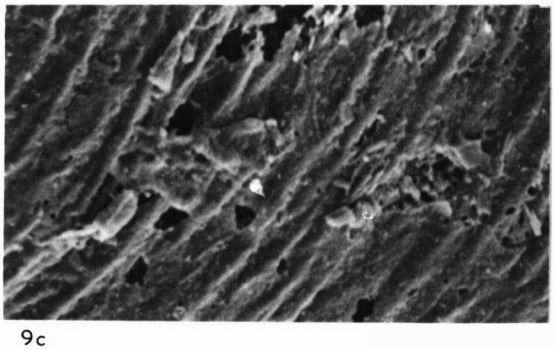
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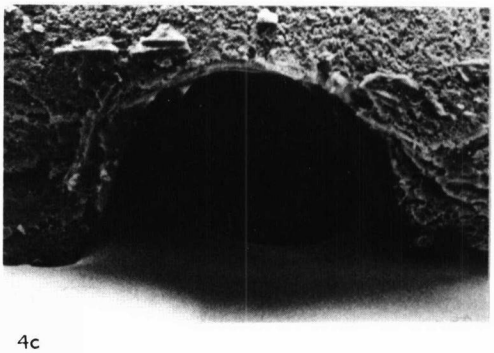
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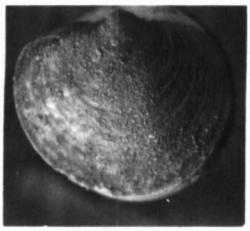
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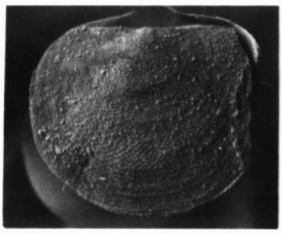
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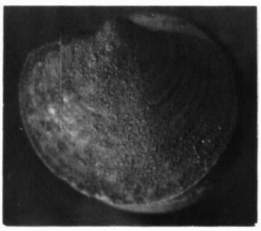
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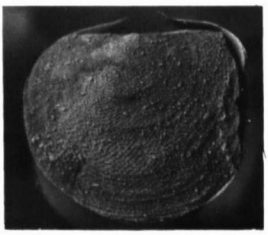
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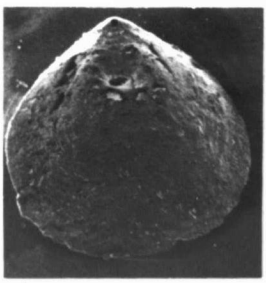
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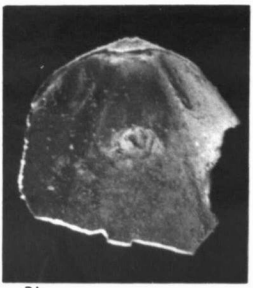
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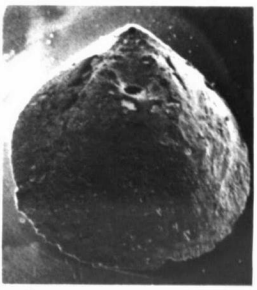
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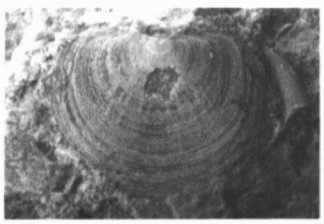
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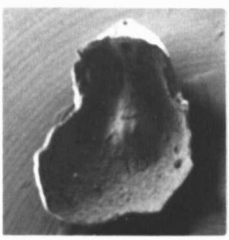
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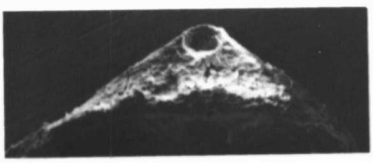
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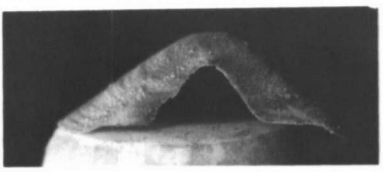
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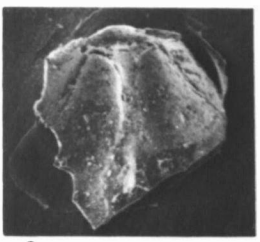
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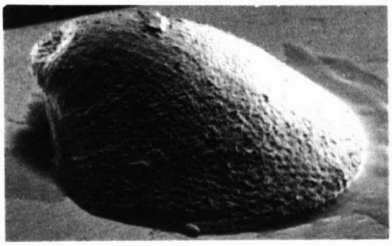

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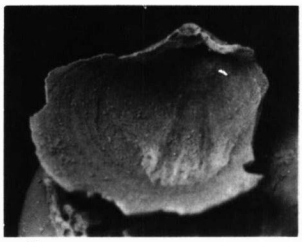

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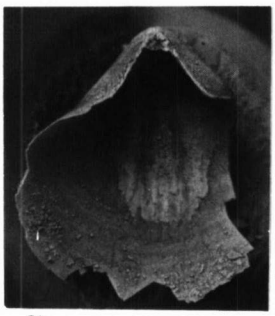

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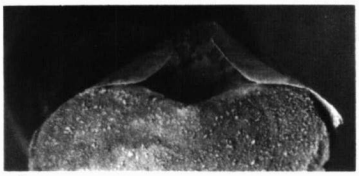

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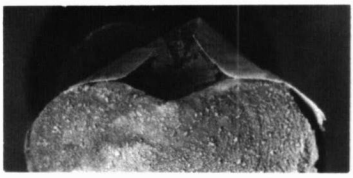

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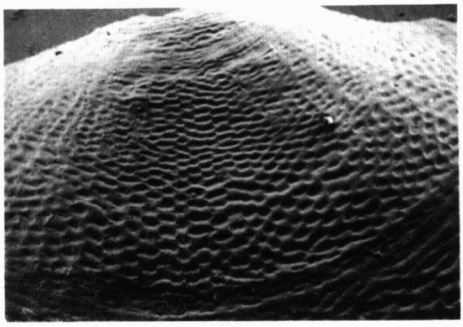

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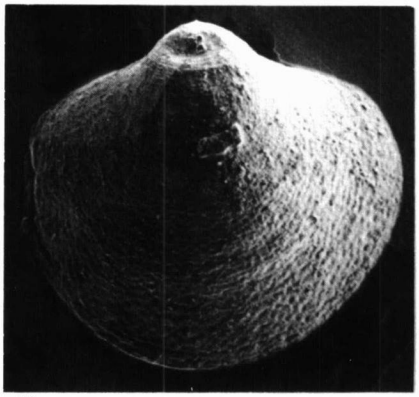

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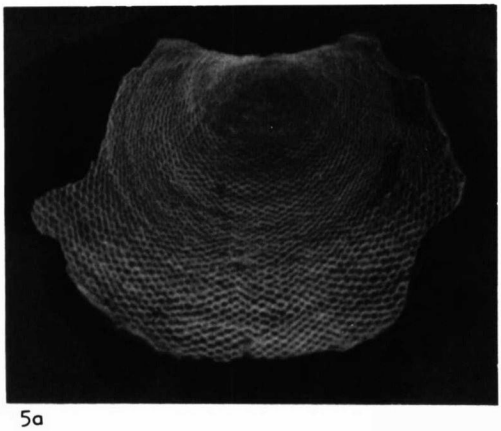

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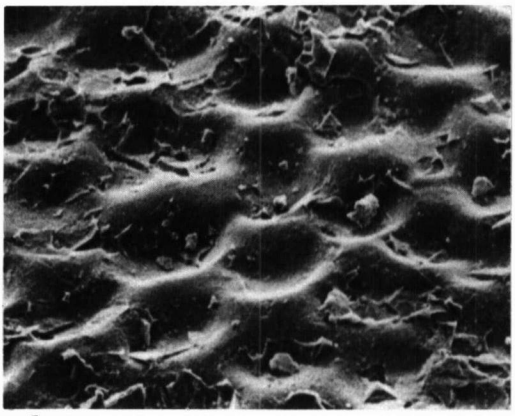

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